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BULLETIN OF THE TORREY BOTANICAL CLUB
VOL. 82, NO. 2, PP. 87–101 MARCH, 1955

CYTOLOGICAL AND EMBRYOLOGICAL STUDIES IN SOLANUM, SECTION TUBERARIUM[1]

RUTH I. WALKER

Studies of gametophyte and seed development have been made for various members of the Solanaceae. Included in these investigations are the studies of Rees-Leonard (1935) and Clarke (1940) for *Solanum tuberosum*. Embryological studies in this family have been summarized by Johansen (1950).

Sterility due to incompatibility following crossing or to the failure of seeds to complete development after fertilization has been reported in the Solanaceae. Blakeslee, Belling and Farnham (1923) observed abortive seeds in *Datura stramonium* following a 4N × 2N cross and a similar condition was reported by Jorgensen (1928) as a result of matings of 4N and 2N races of *Lycopersicon*. Incompatibility between 4N and 2N reciprocal crosses in *Datura stramonium* and between species crosses *D. stramonium* × *D. metel* and *D. stramonium* × *D. certocaula* were studied by Sansome, Satina, and Blakeslee (1942). They found an early post fertilization breakdown of the endosperm and embryo. Cooper and Brink (1940) described the collapse of immature seeds following out crossing of *Nicotiana rustica* to *N. glutinosa*, *Petunia violacea* and *Lycopersicon esculentum*. Later Brink and Cooper (1941) reported the nature of seed collapse following the cross *N. rustica* × *N. tabacum* and again in 1945 following the crosses between certain diploid and tetraploid strains of *Lycopersicon pimpinellifolium* and following crosses between these races and *L. peruvian*. The course of development of the seeds in all these crosses were similar. Seed sterility resulting from certain interspecific crosses between polyploid species in the genus Solanum, section Tuberarium was observed by Lamm 1945. He reported that the cause of the incompatibility was difficult to determine until more species have been investigated. Beamish (1954) described the nature of seed failure following crosses between *S. demissum* (6N) and five diploid species. Seed abortion is attributed to a disturbance in the nutritional balance within the seed.

The present investigation is a study of ovule and seed development of *Solanum demissum* Lindl. (2N = 72) and of seed development following

[1] Supported in part by a grant from the Wisconsin Alumni Foundation.

The writer expresses her appreciation to Dr. R. W. Hougas for the facilities made available at the Inter-regional Potato Introduction Station, Sturgeon Bay, Wisconsin, to Mr. Roman Ross for his care of the plant materials and to Dr. D. C. Cooper for assistance and advice.

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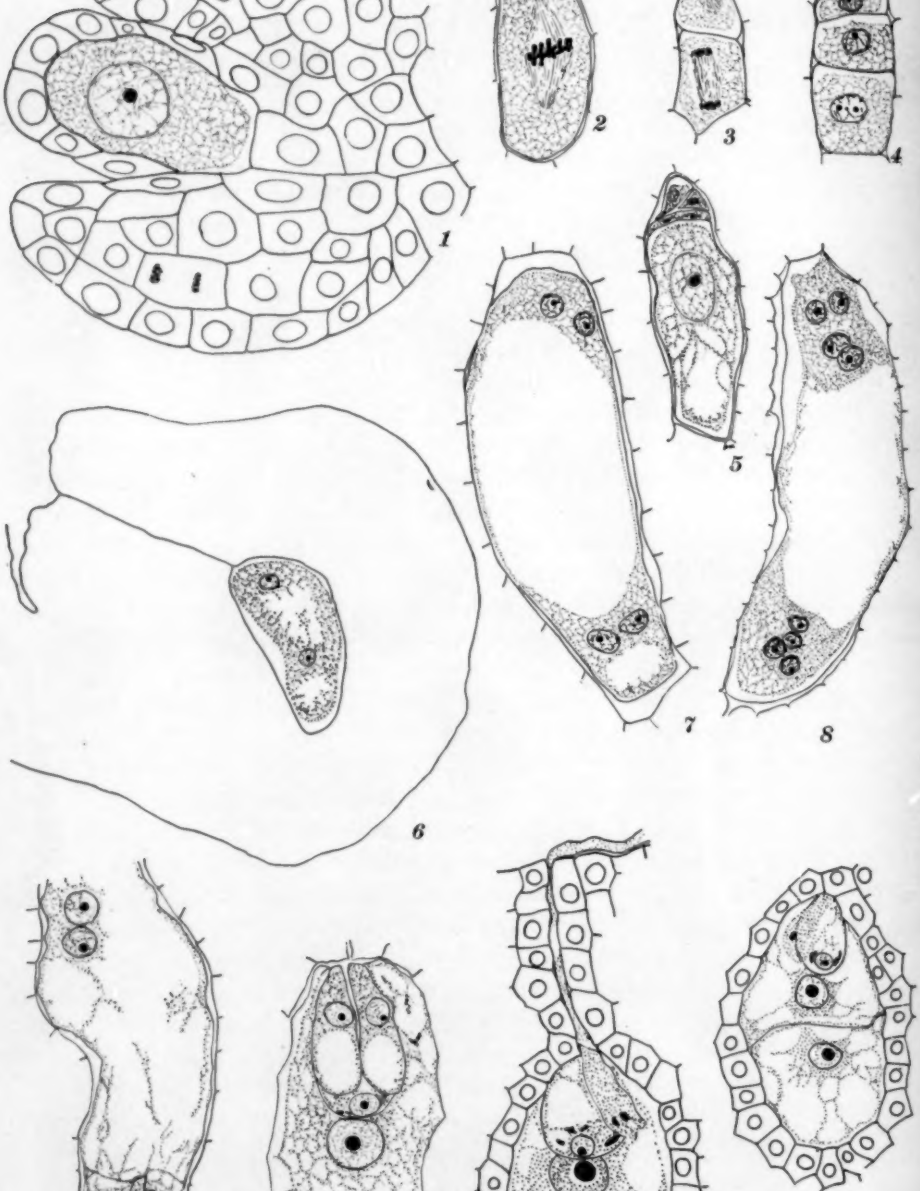
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the matings of this species and certain diploid species namely; *S. polyadenium* Greenm., *S. gibberulosum* Juz., *S. tarijense* Hawkes and *S. Schickii* Juz. et Burk. in an attempt to determine the cause and nature of the incompatibility in the various interspecific crosses.

Materials and methods. Materials for this investigation from above mentioned species were collected from plants growing in the greenhouses and in the field plots of the Inter-regional Potato Introduction Station at Sturgeon Bay, Wisconsin, during the summers of 1952 and 1953. Since *S. demissum* was used as the pistillate plant in this study, buds were collected from field material for early stages of ovule formation and megagametophyte development. Flower buds of *S. demissum* growing in the greenhouse and the field were emasculated and later hand pollinated by using pollen from the different species listed above. Flowers of *S. demissum* were selfed for controls.

Fruits were collected at varying intervals after pollination for stages of the developing seeds. Materials were immersed in Carnoy's alcohol-acetic-chloroform mixture for a few minutes and then transferred to either formalin-acetic acid-alcohol solution, to Randolph's modification of Craf solution, or to alcohol-acetic acid solution. After imbedding in paraffin, sections were cut at 10–20 μ and stained with either Delafield's haematoxylin, Heidenhain's iron haematoxylin, or with safranin and fast green. Fruits arising from the above crosses were also allowed to remain on the plants until maturity, at which time they were collected and dissected to determine the frequency of seed formation.

Ovule and megagametophyte development of Solanum demissum. The ovary of *S. demissum* consists of two fused carpels with an enlarged placenta on which arise many ovules. An ovule first appears as a rounded meristematic mass of cells, the nucellus, from the outer margin of which an integument develops. Growth occurs more rapidly on the side of the ovule toward the apex of the carpel with the result that the ovule bends and assumes an anatropous position.

A single subepidermal cell at the tip of the ovule soon becomes differentiated as the archesporial cell which functions as the megaspore mother

FIGS. 1–12. *Solanum demissum.* FIG. 1. Young ovule with megaspore mother cell. × 750. FIG. 2. Megaspore mother cell with heterotypic equatorial plate. × 750. FIG. 3. Daughter cells during homeotypic division. × 750. FIG. 4. Linear row of four megaspores. × 750. FIGS. 5–10. Stages in development of megagametophyte. FIG. 5. Functional megaspore with three disintegrating megaspores. × 750. FIG. 6. Ovule with two-nucleate megagametophyte. × 400. FIG. 7. Four-nucleate megagametophyte. × 750. FIG. 8. Eight-nucleate megagametophyte. × 750. FIG. 9. Chalazal portion of megagametophyte with antipodals and polar nuclei. × 750. FIG. 10. Egg, synergids and primary endosperm nucleus formed from fusion of polar nuclei. × 750. FIG. 11. Portion of ovule showing pollen tube in micropyle at forty-eight hours. × 400. FIG. 12. Zygote and two-celled endosperm at forty-eight hours. × 400.

cell. This cell is easily recognized by its greater size and its deeper staining properties. The megaspore mother cell continues to grow until it is about three times as long as broad (fig. 1). The integument begins its development as a meristematic outgrowth of the nucellus at a level just below that of the archesporial cell and continues to grow around the apical portion of the nucellus. By the time meiosis is completed the single integumen has become six to ten layers of cells in thickness and completely surrounds the nucellus. Provascular tissue is not visible at this time, but a few cells in the chalazal region are differentiated as the chalazal pocket or hypostase. These cells have thick refractive walls and their contents appear to be plasmolyzed. Early in the development of the ovule the megaspore mother cell undergoes meiosis (fig. 2). As a result of the first division two daughter cells are formed (fig. 3). A second division quickly follows forming a linear row of four megaspores. The chalazal spore forms the megagametophyte; the other three spores disintegrate (fig. 5).

The functional megaspore rapidly increases in size. Its nucleus undergoes three successive nuclear divisions (figs. 6, 7) which result in the typical eight-nucleate condition (fig. 8). Cell walls are formed and an eight-nucleate seven-celled megagametophyte is formed.

The egg apparatus at the micropylar end of the megagametophyte consists of three (more or less) pear-shaped cells, the two synergids and the egg (fig. 10). The apical portion of each synergid is beak-like and contains dense cytoplasm in which is embedded a large nucleus. At the basal portion of each synergid is a large vacuole. The egg cell extends into the megagametophyte beyond the synergids. The broad basal portion contains the nucleus surrounded by cytoplasm and a large vacuole occupies the apical portion of the egg cell. The three antipodals at the chalazal end of the megagametophyte (fig. 9) become elongated and then disintegrate. The polar nuclei migrate to a position just posterior to the egg cell, where they come in contact and fuse prior to fertilization (fig. 10). Food reserves in form of starch are present in the vicinity of the primary endosperm nucleus. During the growth of the megagametophyte, apical and lateral cells of the nucellus degenerate. Cells of the inner layer of the integument, the endothelium, surround the megagametophyte. This development of the ovule and megagametophyte is in general similar to that described by Rees-Leonard (1935) Clarke (1940) for *S. tuberosum*.

Fertilization, endosperm and embryo development following self pollination. Pollen tubes are present in great numbers in the ovary cavity and on the surface of the placenta and ovules approximately twenty-four hours after pollination. A tube passes through the micropyle and enters the megagametophyte between the synergids and egg. The synergids are disorganized by the entrance of the pollen tube and remnants of the tube with

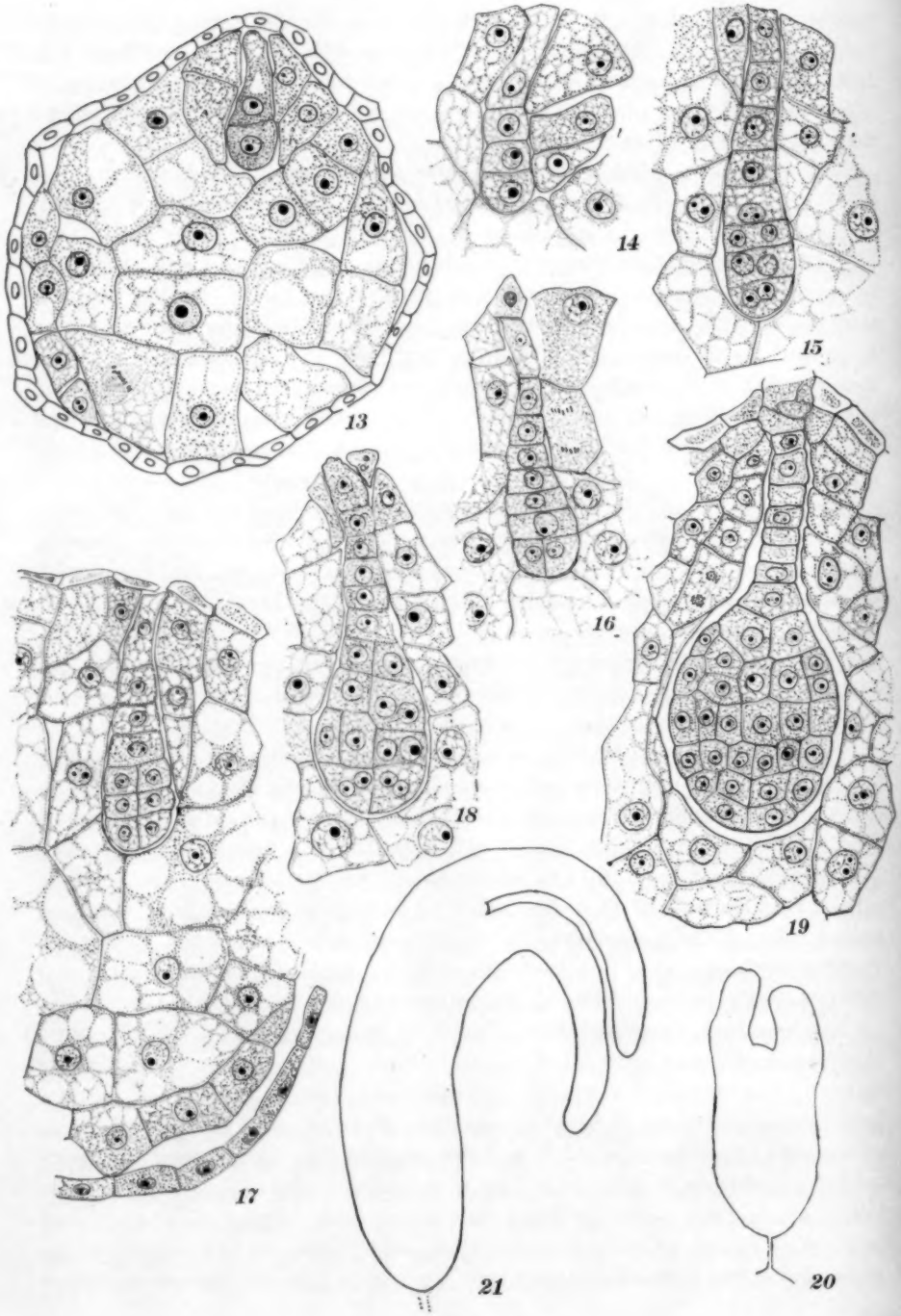
darkly stained bodies may be present (fig. 11). These bodies are similar to the "x bodies" occurring in Petunia (Cooper 1946). In the course of fertilization one male nucleus unites with the egg nucleus and the other unites with the fused polar nuclei. This process takes place between twenty-four to forty-eight hours after pollination.

The endosperm of *S. demissum* is the cellular type. The primary endosperm nucleus divides shortly after fertilization and a cell plate is formed. A two-celled endosperm is present at forty-eight hours after pollination (fig. 12). Further divisions of the endosperm occur rapidly and the endosperm usually consists of approximately thirty-two cells (fig. 13) by the time the division of the zygote has occurred. The cells of the endosperm are large and highly vacuolate. Following fertilization and accompanying the development of the embryo and endosperm there is an increase in size of the whole ovule due to active division of the cells in the endothelium, the funiculus, and the outer layers of the integument. The inner integumentary cells disintegrate.

The endothelial cells become elongate and contain a single centrally located nucleus surrounded by cytoplasm. The cells between the vascular bundle in the funiculus and the chalazal pocket are elongate and filled with dense cytoplasm which is in sharp contrast to the highly vacuolate surrounding cells. Some of these cells later become differentiated into conductive tissue which connects the vascular tissue of the placenta with the chalazal pocket. Vascular strands become differentiated in the funiculus connecting the mature vascular tissue of the placenta with that of the seed.

The embryo development of *Solanum demissum* resembles that described by Bhaduri (1936) as commonly occurring in *Physalis minima*. The zygote divides transversely to form a two-celled proembryo consisting of a small apical cell and an enlarged basal cell (fig. 13). By successive transverse divisions of these cells (fig 14) and their derivatives a linear row of eight cells is usually formed (figs. 15, 16). The embryo is formed from the four apical cells of the proembryo, the four basal cells become the suspensor. Further divisions occur in some of its cells, the plane of division being transverse so that at maturity the suspensor consists of six to eight cells.

Longitudinal divisions occur in the four apical cells (figs. 16, 17). Further transverse and vertical divisions follow resulting in a sphere shape embryo (figs. 18, 19,). With the continued multiplication of cells, the embryo becomes longer and broader especially at the apex. Certain peripheral cells on the opposite sides of the embryo near its apex become actively meristematic and form two outgrowths, the cotyledons (fig. 20). The basal portion of the embryo below the cotyledons becomes the hypocotyl. The epicotyl is a small apical protuberance between the cotyledons. At maturity the hypocotyl shows a well-developed root cap region. The cotyledons are coiled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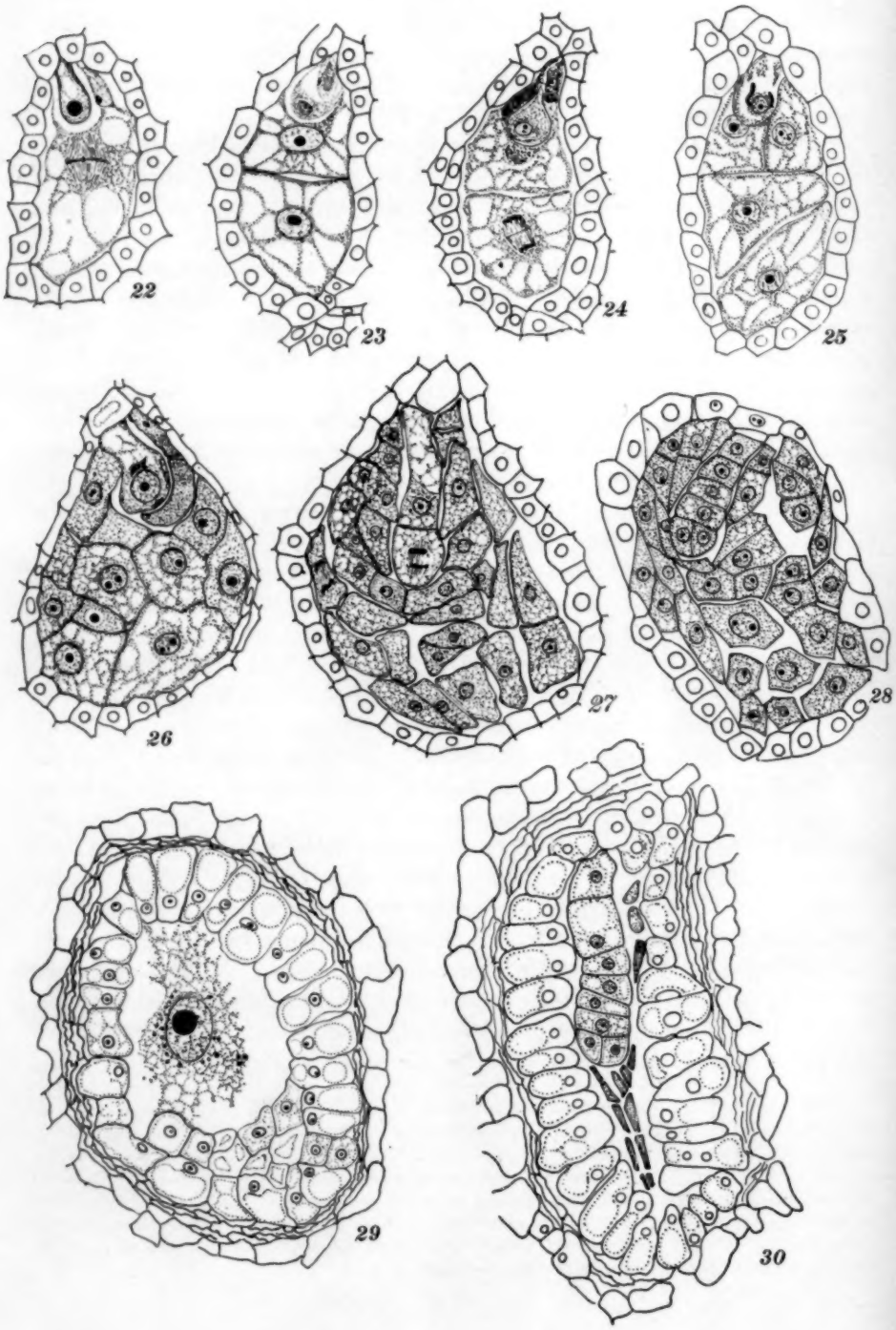
at their terminal portion and the epicotyl is a small and inconspicuous structure between them at the apex of the embryo. The cotyledons and hypocotyl elongate rapidly and during their development, the embryo curves in the region of the epicotyl (fig. 21).

Solanum demissum × S. polyadenium. Many investigators have attempted, without much success, to obtain hybrids between *S. polyadenium* (2n = 24) with other species of *Solanum*. During the summers of 1952 and 1953 numerous crosses were made using *S. demissum* as the pistillate parent. Pollen of *S. polyadenium* from various sources was used on the stigmas of previously emasculated *S. demissum* flowers. Pedicels and ovaries of some of these were sprayed several times with a .0025 per cent solution of naphthaleneacetic acid to prevent abscission and to stimulate further development of embryo and endosperm if fertilization did occur. In no instance were embryos formed. Untreated pistils remained on the plant eight to ten days while some of the treated pistils underwent limited growth and did not abscise until twenty-eight days.

Examinations of longitudinal sections of untreated *S. demissum* pistils were made forty-eight hours after pollination and pollen tubes were found to have penetrated the style only a short distance. No trace of pollen tubes were found in the ovarian cavity. Another attempt to obtain fertilization was made by removing the stigmas from pistils of *S. demissum* and placing a mixture of macerated stigmas of *S. polyadenium* and gelatine-agar with sugar on the cut surface of the decapitated style. This was then covered with *S. polyadenium* pollen. Seeds did not develop. Since Lamm (1945) had reported that failure of certain crosses could be overcome by grafting the female parent on the tomato as in the case of *S. chaucha* × *S. tuberosum*, *S. demissum* was grafted on *Lycopersicon esculentum* var. Bonny Best according to the method described by Jorgensen and Crane (1927) and Jorgensen (1928). Young *S. demissum* shoots were cleft grafted on tomato stocks about $\frac{1}{4}''$ in diameter. The grafts were wrapped with electrician's tape. Only a few leaves were left on the tomato plants and when the graft was well established all leaves of tomato were removed. These plants were grown for the most part in the greenhouse although a few were transported to the field. Flowers of the *S. demissum* scion previously emasculated were pollinated with *S. polyadenium* pollen. No seeds were formed which prob-

FIGS. 13–21. Stages in development of the embryo. FIG. 13. Two-celled proembryo at five days. × 400. FIG. 14. Four-celled proembryo at six days. × 400. FIG. 15. Four-celled embryo and four-celled suspensor at seven days. Nuclei of three apical cells of embryo divided. × 400. FIG. 16. Embryo with endosperm at seven days. × 400. FIG. 17. Embryo with adjacent endosperm and endothelium at seven days. × 400. FIG. 18. Older embryo at ten days. × 400. FIG. 19. Slightly older embryo with dermatogen differentiated at ten days. × 400. FIG. 20. Embryo with well-differentiated cotyledons at fourteen days. × 75. FIG. 21. Nearly mature embryo at twenty-one days. × 75.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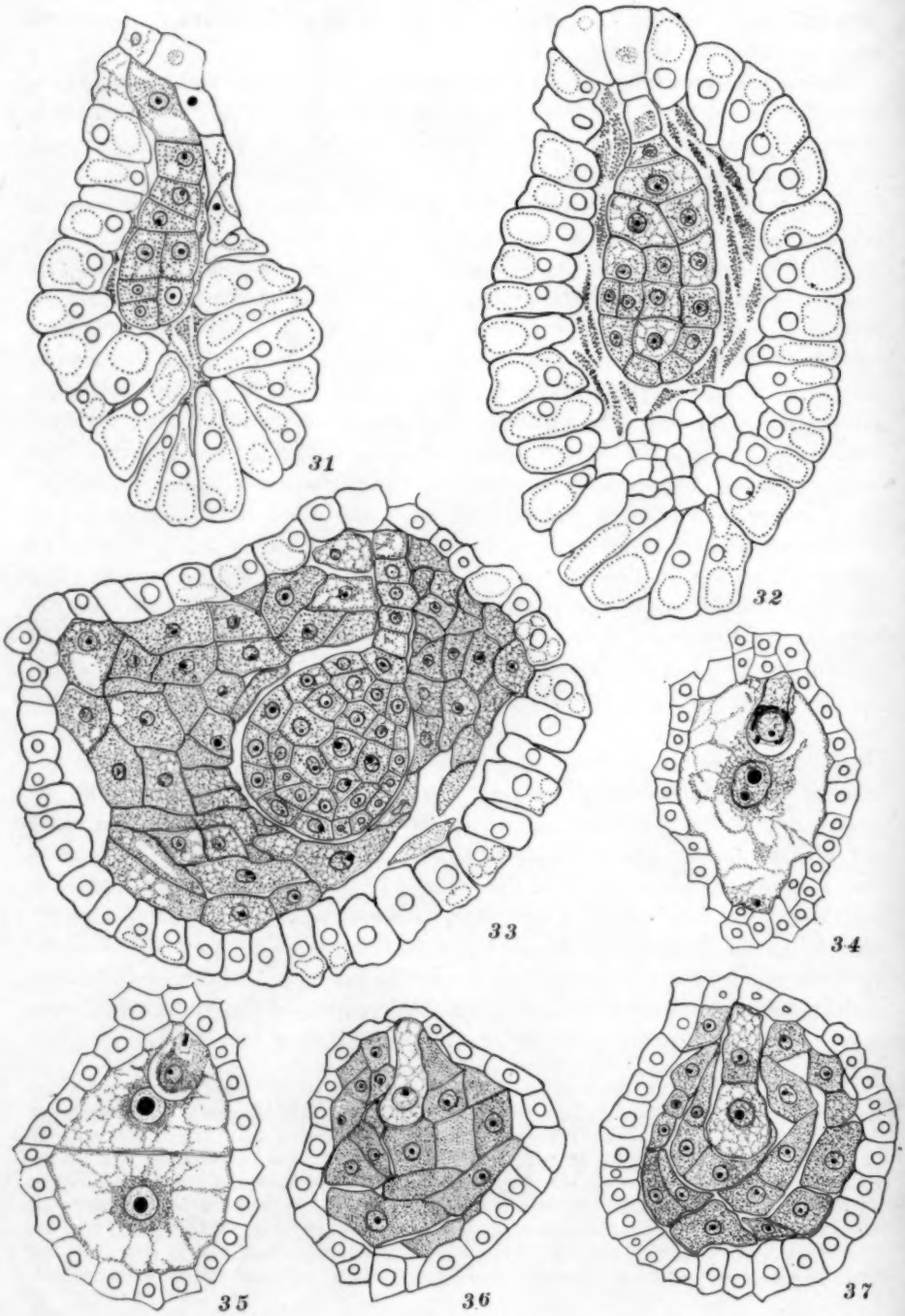
ably indicated that the Lycopersicon stock had no effect on the *S. demissum* scion in bringing about fertilization.

Solanum demissum × S. gibberulosum. Very few viable seeds are formed as a result of this cross. In mature fruits resulting from this cross seeds were present in only 12 of the 130 fruits examined, the average number of seeds per fruit was 5.5.

Pollen tubes are visible in the ovarian cavity about forty-five hours after pollination and some of the ovules are already fertilized at this interval. Pollen tubes may continue to be visible up to five days after pollination. After fertilization a two-celled endosperm is formed as a result of the division of the primary endosperm cell (figs. 22, 23, 24). Other nuclear and cell divisions occur but at a less rapid rate than in the normally developing seed (fig. 25). The hybrid zygote has not divided (fig. 26) at six days after pollination while in controls a four-celled embryo is present at this interval (fig. 14). As the cells of the endosperm are dividing and growing, the maternal cells immediately surrounding the endosperm, the endothelium, likewise are increasing in size and dividing, the plane of division being at right angles to the long axis of the ovule. Their nuclei are centrally located and surrounded by cytoplasm. When the endosperm has reached the thirty-two celled stage, the zygote undergoes division. This usually occurs between six and seven days after pollination, although instances are noted of two- or three-celled embryos in this same material. The cells of the endosperm are smaller and their cytoplasm is dense and takes a deeper stain than those in the control (fig. 27).

The entire ovule proceeds to grow slowly. Marked changes occur in the cells of the endothelium as seen in figures 28, 29 and 30. These cells increase greatly in size forming finger-like projections which extend into the central cavity. Large vacuoles appear to have pushed the nucleus to that side of the cell adjacent to the endosperm. Occasionally the endothelial cells divide so that this structure is two rows of cells in thickness (figs. 29, 32). With the increase in size of the endothelium cells, the cells of endosperm are absorbed first in the vicinity of the embryo. Ultimately the entire endosperm disintegrates. This hyperplastic growth of the endothelium has severed the connection between the chalazal pocket and the endosperm.

FIGS. 22–30. *Solanum demissum* × *S. gibberulosum*. FIG. 22. Zygote. Endosperm nucleus in process of division at forty-five hours. × 400. FIG. 23. Two-celled endosperm at forty-eight hours. × 400. FIG. 24. Second division of endosperm cells. Zygote and remains of synergids and pollen tube at forty-eight hours. × 400. FIG. 25. Zygote with multicellular endosperm at five days. × 400. FIG. 26. Zygote and endosperm tissue at six days. × 400. FIG. 27. Two-celled embryo surrounded with small dense cells of endosperm at seven days. × 400. FIG. 28. Older embryo, with endosperm at eleven days. × 400. Fig. 29. Transverse section through endosperm and endothelium at fourteen days. × 400. FIG. 30. Embryo with disintegrating endosperm and hyperplasia of endothelium at fourteen days. × 400.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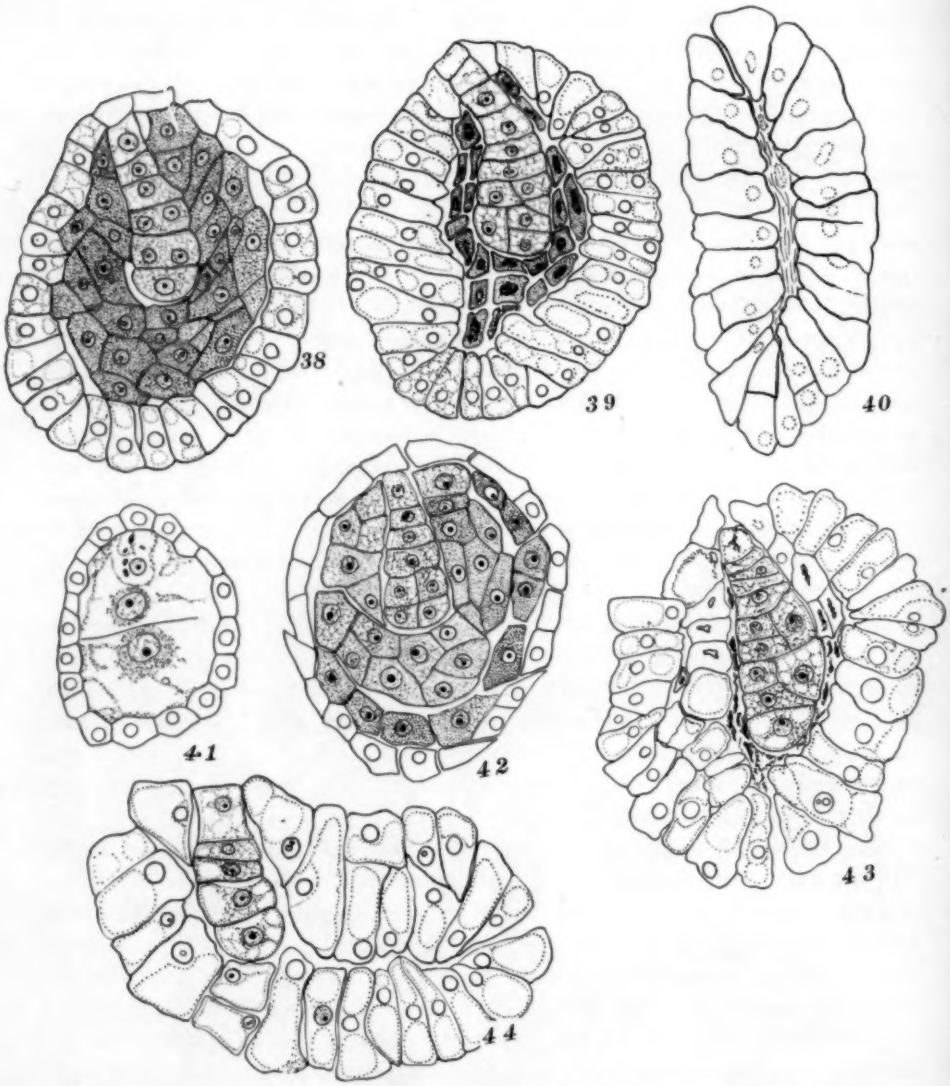
This visibly effects the rate of growth of the embryo and eventually it ceases to enlarge and the seed fails to undergo any further development. The abortion of the embryo is not limited to any one period but may occur at any stage in the development of the seed. Varying stages of development of the embryo and endosperm are present fourteen days after pollination (figs. 29–33). In figure 33 the embryo has reached the spherical stage of development and it is highly probable that it will continue to develop for some time whereas the embryos depicted in figures 30, 31, and 32 have attained a limited number of cells and are still in a linear stage of development. These cells are characterized by vacuolate cytoplasms, which gives a starved appearance to the embryo. The endosperm is in varying stages of depletion as a result of its inability to grow and expand. In some instances even the initial stage of division seems to be inhibited (fig. 29). All this is in marked contrast to the control seed, *S. demissum* selfed, which has an endothelium layer of flattened cells, a well-developed endosperm and embryo with well-differentiated cotyledons. An explanation for the difference in number of seeds maturing after self and cross pollination may in part be due to the restricted pollen tube growth, and to the failure of embryo to develop to maturity.

Solanum demissum × S. tarijense and S. demissum × S. Schickii. Partial sterility due to seed failure following fertilization likewise results from these crosses. Of the 50 fruits obtained as a result of the cross *S. demissum* × *S. tarijense,* 41 contained seeds with an average of 1.8 seeds per fruit, while 21 of the 37 fruits resulting from cross *S. demissum* × *S. Schickii* possessed seeds averaging about 1.7 seeds per fruit. The viability of these seeds has not been determined.

The cause of seed failure following these crosses is similar to that found following the cross *S. demissum* × *S. gibberulosum.* In both instances pollen tubes are visible in the ovarian cavity and fertilization is effected approximately forty-eight hours after pollination (fig. 34). The first division of the endosperm immediately follows (figs. 35, 41) while the zygote divides about six days later (figs. 36, 37). The endosperm and embryo continue to grow slowly (figs. 38, 39, 42), while the endothelium is in a more active meristematic condition. Divisions in the cells of endothelium occur at right angles to the long axis of the seed. Following the cross *S. demissum* × *S.*

FIGS. 31–33. *Solanum demissum* × *S. gibberulosum.* FIGS. 34–37. *S. demissum* × *S. Schickii.* FIG. 31. Older embryo with remnants of endosperm at fourteen days. × 400. FIG. 32. The same but with embryo in more advanced stage of development at fourteen days. × 400. FIG. 33. Spherical embryo surrounded by endosperm cells with dense contents and endothelium showing beginnings of hyperplasia at fourteen days. × 400. FIG. 34. double fertilization at forty-eight hours. × 400. FIG. 35. Zygote and two-celled endosperm at sixty-six hours. × 400. FIG. 36. Zygote with endosperm at forty-eight hours. × 400. FIG. 37. Two-celled embryo with dense endosperm and endothelium showing beginnings of hyperplasia at five days. × 400.



FIGS. 38–41. *S. demissum* × *S. Schickii*. FIGS. 41–44. *S. demissum* × *S. tarijense*. FIG. 38. Older embryo and endothelial cells enlarged at seven days. × 400. FIG. 39. Embryo with disintegrating endosperm and proliferating endothelium at ten days. × 400. FIG. 40. Hyperplastic endothelium surrounding remnants of disintegrating endosperm and embryo at fourteen days. × 400. FIG. 41. Zygote and two-celled endosperm at forty-eight hours. × 400. FIG. 42. Multicellular endosperm and embryo at seven days. × 400. FIG. 43. Embryo with remains of disintegrated endosperm and hyperplastic endothelium at ten days. × 400. FIG. 44. Embryo and endothelium enlarged at fourteen days. × 400.

tarijense divisions also occur parallel to long axis of the seed, resulting in an endothelial tissue that is several layers of cells in thickness in certain areas. As growth proceeds, the hyperplasia of the endothelium absorbs the cells of the endosperm and the embryo ceases to grow (figs. 40, 43, 44). The collapse of the embryo is usually completed following the cross *S. demissum* × *S. Schickii* in 12 days and following the crosses *S. demissum* × *S. gibberulosum* and *S. demissum* × *S. tarijense* in about 14 days.

Discussion. It would appear that seed sterility between the species crosses herein described is a matter of degree. Following the cross *S. demissum* × *S. polyadenium* fertilization does not occur. Since abortive pollen has often been associated with sterility, samples of pollen grains were observed to determine if the pollen grains were irregular. Counts were made and the pollen was found to be from 43 to 63% normal. The pollen germinated readily on agar-gelatine mixture containing sugar. In one case short pollen tubes were observed in the stigma of *S. demissum*. Failure of fertilization is apparently due to inability of pollen tubes to reach the ovules.

In the other crosses, *S. demissum* × *S. gibberulosum*, *S. demissum* × *S. tarijense* and *S. demissum* × *S. Schickii*, fertilization occurs in many ovules but only a few seeds develop normally. This type of sterility in which fertilization occurs but the young embryos do not develop beyond a certain stage following wide crosses has been reported in a number of other Solanaceous plants. Sansome, Satina, Blakeslee (1942) and Satina, Rappaport and Blakeslee (1950) found a similar condition existed as a result of certain interspecific crosses in Datura. No definite conclusion was reached in regard to the sequence in which the different tissues begin to degenerate or to the factors causing the disintegration. Cooper and Brink (1940), and Brink and Cooper (1941) described seed development following certain incompatible species crosses in *Nicotiana* and in (1945) following crosses between certain strains of *Lycopersicon pimpinellifolium*. They attribute the collapse of the embryo to be the result of retarded endosperm growth, extreme hyperplasia of the nucellus and failure of some of the integument cells between the apex of the vascular bundle and the chalazal pocket to differentiate into conductive tissue. Beamish (1954) reported abortive seed formation following matings between *S. demissum* (6n) and five diploid *Solanum* species. The results obtained are in general similar to those found in this investigation.

In the species studied in this investigation in which fertilization is effected, the process is typical and is followed by a division of the endosperm. The zygote does not divide until the endosperm has undergone five or six divisions which is from six to seven days after pollination. After the first division of the zygote there is a slowing down in the divisions of the endosperm in comparison with the control. The hybrid embryos grow

and may reach varying stages of development before collapse. The cells of the embryo are large, vacuolate, and the entire structure has a starved appearance. The rate of growth is definitely retarded as compared with that of the controls. A hybrid embryo two weeks after pollination may be linear or spherical whereas an embryo resulting from selfing will probably have well-differentiated cotyledons.

During the early stages of development of the hybrid embryos starch is present in great abundance in the placenta and ovary wall. As growth proceeds, the starch disappears from the central placental region and is found within the integuments. The presence of food within the cells of the seed indicates that failure of seed development is not due to an absence of food but the fact that such food is not available to the embryo. Cells between vascular tissue and chalazal pocket are not as elongated as in control material which may in part inhibit translocation of the nutrients to the endosperm. The collapse of seed is due to starvation of embryo which is associated with the absorption of the endosperm by the hyperplastic functioning of the endothelium.

SUMMARY

1. A single hypodermal cell is differentiated as an archesporial cell in *Solanum demissum*. This functions directly as the megaspore mother cell.

2. A linear row of four megaspores is formed, the chalazal spore develops into an eight-nucleate, seven-celled megagametophyte; the other megaspores disintegrate.

3. Double fertilization occurs between 24–48 hours after self pollination. The endosperm cells divide rapidly forming large highly vacuolate cells.

4. Division of the zygote occurs when the endosperm consists of about thirty-two cells. Successive transverse divisions of the proembryo follow resulting in a linear row of eight cells. An embryo with hypocotyl, two lateral cotyledons and terminal epicotyl is formed from the four apical cells. The four basal cells of the proembryo undergo some further transverse divisions to form the suspensor.

5. A restricted pollen tube growth and failure of fertilization occurs following the cross *S. demissum* × *S. polyadenium*.

6. Partial sterility following the crosses *S. demissum* × *S. gibberulosum*, *S. demissum* × *S. tarijense* and *S. demissum* × *S. Schickii* occurs.

7. Double fertilization although somewhat delayed in comparison to *S. demissum* selfed, occurs in each instance.

8. Hybrid endosperm cells grow slowly and following successive divisions the cells become smaller.

9. Division of the zygote is delayed and the embryo seldom develops beyond a relatively few celled stage.

10. The cells of the endothelium proliferate producing large outgrowths which extend into the region occupied by the endosperm.

11. A large quantity of starch is present in the placenta and in the integuments of developing normal and hybrid seeds.

12. Collapse of some of the hybrid seed is due to the inability of the endosperm to absorb and in turn to supply these materials to the embryo. The retardation of the development of the endosperm is associated with the hyperplastic growth of the cells of the endothelium.

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THE RUST GENERA ALLOTELIUM, ATELOCAUDA, COINOSTELIUM AND MONOSPORIDIUM[1]

M. J. THIRUMALACHAR AND FRANK D. KERN

It is with satisfaction that we are able to present these studies toward a better understanding of certain rust genera.

(1) **Structure of the telium in Allotelium.** The genus *Allotelium* was described by Sydow (1939) for a rust on *Calliandra trinervia* Benth. collected by him in Ecuador, South America. Only telia were observed and were described as subepidermal, erumpent and bordered by a multiseriate persistent "peridial" layer. The teliospores were characterized as pedicellate, chestnut-brown, and vertically septate, as in *Diorchidium* Kalchbr., from which it was differentiated chiefly by its multiseriate "peridia." The specimens of *Allotelium mirabile* Sydow, the type and only known species, were believed to have been lost during the bombing of Berlin in the second world war. Consequently our knowledge has been restricted to the descriptions given by Sydow.

Fortunately, however, the type material (Sydow, Fungi Exotici Exsiccati 1108, Ecuador, Puyo Prov. Napo-Pastaza, 24-2-1938, leg. H. Sydow on *Calliandra trinervia* Benth.) was located by the senior author at the Naturhistorisk-riksmuseet, Stockholm, Sweden, where most of the collections by the late H. Sydow are deposited. Through the kindness of the Director, Dr. E. Hütner, opportunity to examine the type of *Allotelium mirabile* became available and further information on the genus can now be presented.

The infection on the leaves appear as shining black pin points, sparsely distributed and surrounded by a hypersensitive halo (fig. 1). Most of the sori are very heavily parasitized by *Darluca filum*. The telium initials are formed by the grouping of plectenchymatic layers within the epidermis, the teliospores being differentiated deep in the sorus. The outer overlying layers of hyphal cells beneath the cuticle become thick-walled and develop a yellowish-brown color (fig. 2). As the sorus matures, the cuticle, the outer wall of epidermis and the two to three layers of thick-walled hyphal cells rupture, exposing the teliospores. The thickened persistent hyphal cells bordering the sorus (fig. 3) afford protection to the developing spores in the same way as do peridial layers of *Aecidium*.

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Sydow designated these persistent hyphal cell-layers as a "peridium," with which they are functionally similar. However, morphological and ontogenetic considerations warrant the distinction between a true peridium

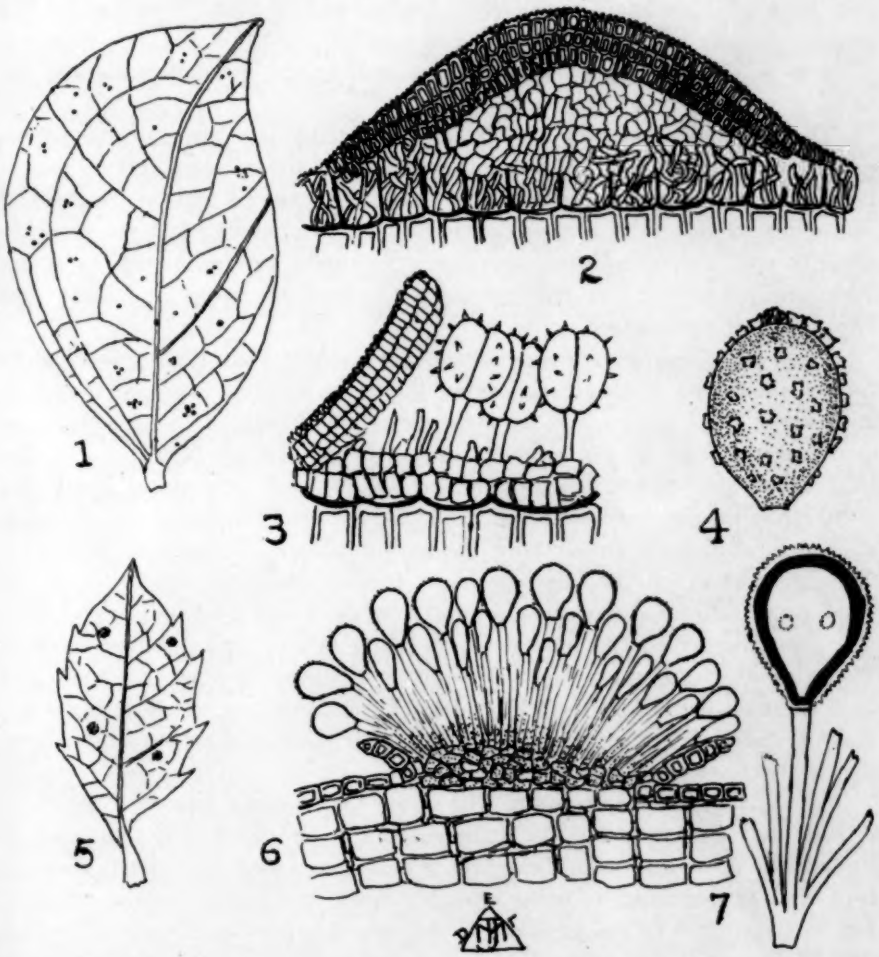

FIG. 1. Infected leaf of *Calliandra trinervia* with telia of *Allotelium mirabile* (type material), natural size. FIG. 2. Young telium × 360. FIG. 3. Mature telium with spores × 360. FIG. 4. Teliospore of *Pileolaria incrustans* (from type) × 720. FIG. 5. Infected leaf of *Cithraxylon illicifolium* with sori of *Coinostelium quitense* (type material), natural size. FIG. 6. Section through uredium × 360. FIG. 7. Showing clustered nature of urediospores on sporogenous basal cell × 720.

and the cell-layers bordering the sorus in *Allotelium*. While the term "peridium" is used in a different sense in the various groups of fungi, in the case of plant rusts the peridial layer is formed by the outermost layer

of spores becoming transformed into a sterile tissue of thick-walled cells. Peridia are known in the aecia of *Aecidium* and *Peridermium;* uredia of *Hyalopsora, Milesina, Melampsorella, Melampsoridium, Pucciniastrum;* and telia of *Pucciniosira, Dietelia, Endophylloides,* and *Gambleola.* The peridia usually are strongly developed and border the sorus, but in a few cases as in *Gambleola* and *Endophylloides* they are inconspicuous and are carried over the telial column.

The multilayered thick-walled cells bordering the sorus in *Allotelium* are not transformed spores, but rather belong to the upper plectenchymatic layer differentiated during the early stages of sorus formation. In most of the genera where telia are non-peridiate the plectenchymatic tissue above remains thin-walled and disintegrates at maturity leaving an empty space. The teliospores that are differentiated occupy this space and, after the rupture of the sorus, are exposed.

From the foregoing consideration it is evident that the sorus in *Allotelium* should be distinguished from the true peridial type as known in *Aecidium, Pucciniosira,* etc. It is proposed to designate the multilayered structures of thick-walled cells as "dermata" as distinct from peridia. The telia are therefore intra-epidermal, erumpent, and dermatate. While the occurrence or non-occurrence of peridia has been considerd in rust taxonomy as of generic importance the significance of dermata is unknown. They may be given the same status as the stockade-like structures in the uredia and telia of the genus *Corbulospora* described by Cummins (1940).

Sydow described the teliospores as being binate on a common pedicel. This gives the impression that the two cells of the spore arise independently on a common pedicel and are laterally united. However, the teliospores are actually 2-celled being vertically septate as in *Diorchidium* and not binate in the strict sense of the term.

(2) **The genus Atelocauda.** The genus *Atelocauda* was established by Arthur and Cummins (1933) for a rust on *Lonchocarpus* sp. collected in Panama by J. R. Johnston. The genus is monotypic with *A. incrustans* as the type. It was described as being closely related to *Uromyces* from which it was distinguished by the presence of subcuticular pycnia in contrast to subepidermal ones in *Uromyces.* The teliospores have digitate cubical warts on the epispore reminiscent of the sculpturings of the teliospores of *Dicheirinia* and *Trachyspora.* Cummins (1937) stated that *Atelocauda incrustans* "might, with considerable justification, be considered as directly derived from *Dicheirinia* by continued simplification. Since the teliospores are reduced to single cells it would seem logical that the pedicels should also become unicellular structures." Thirumalachar and Mundkur (1949) pointed out that *Atelocauda* lacks apical cells of the pedicel, so characteristic of the genus *Dicheirinia.*

In making a comparative study of rust genera that occur on Leguminosae it was observed that some of the species that occur on Mimosae were identical with *Atelocauda*. It was first pointed out by Dietel (1928) that in *Pileolaria phyllodiorum* (Berk. & Cke.) Diet. on *Acacia* in Australia, the teliospores have digitate cubical warts. In combination with the subcuticular nature of the pycnia, Dietel showed that *Pileolaria* closely resembled *Dicheirinia* and *Uromycladium* and placed it in the tribe Raveneliae. A detailed examination of the teliospores of *Atelocauda incrustans* from the type material (fig. 4) and of *Pileolaria phyllodiorum* along with other species of *Pileolaria* indicates that there are no distinguishing characters to separate *Atelocauda* from *Pileolaria*. *Atelocauda* is therefore reduced to synonymy with the earlier described *Pileolaria*, *Atelocauda incrustans* Arthur and Cummins becoming **Pileolaria incrustans** (Arthur and Cummins) comb. nov.

(3) **The genus Coinostelium.** In 1939, Sydow described *Coinostelium* as a new genus of rust from Ecuador, parasitizing the leaves of *Cithraxylon illicifolia* HBK. a member of the Verbenaceae. Only uredia were described for the rust; the chief distinguishing characters being that the urediospores and *Puccinia*-like teliospores (in uredia) were born in clusters on sporogenous basal cells. Thirumalachar and Mundkur (1950) previously placed the genus *Coinostelium* as a synonym of *Prospodium*, on the basis of descriptions given by Sydow (1939). The type material of *Coinostelium*, which is *C. quitense* Sydow (Sydow, Fungi Exotici Exsiccati 1098), has been unavailable to most students of the rust fungi but was found deposited along with that of *Allotelium*, and opportunity for examination was afforded through the kindness of Dr. Hütner of the Naturhistorisk-riksmuseet, Stockholm. Studies have confirmed the opinion that *Coinostelium* should be treated as a synonym of *Prospodium* and some of the important details are here presented. The infection on the leaves is sparse, producing pulvinate brown powdery sori. Only uredinia were present in the material available but a few teliospores developing within old uredia were observed. The uredia are subepidermal, erumpent, and pulvinate (fig. 6). The urediospores are formed in fascicles of 6 to 12 on sporogenous basal cells (fig. 7). The basal cells are easily separable from the sorus bed, and in each cluster there are spores of varying maturity. When the teliospores are produced, they are formed similarly on sporogenous basal cells.

The urediospores are pyriform, bilaminate, and unicapitate. The outer wall is paler in color and verrucose, and the inner wall is colored. The urediospores have two equatorial pores, characteristic of the species of *Prospodium*. The teliospores are *Puccinia*-like, pedicellate, and verrucose.

From a consideration of these characters it is evident that *Coinostelium* is generically like *Prospodium*, which occurs mainly on species of the Big-

noniaceae and Verbenaceae. Cummins (1940) who made a monographic study of *Prospodium*, recognized three sections. **Prospodium quitense** (Sydow) comb. nov. (*Coinostelium quitense* Sydow) belongs to the section Euprospodium, allocated for macrocyclic species with subepidermal uredia and telia.

(4) **Monosporidium as a valid genus.** The genus *Monosporidium* was described by Barclay (1887) to accommodate two euphorbiaceous rusts collected in Simla, India. Two species were described, *M. andrachnis* and *M. euphorbiae*, being characterized by an aecidioid telium as in *Endophyllum*, but which on germination of the spores produced a promycelium bearing a single sporidium. Since the genus was based on the germination of the aecidioid teliospore in having a single sporidium, there has been considerable doubt about its validity. Dietel (1928) considered it a synonym of *Aecidium*. Thirumalachar and Mundkur (1949) stated that in *Endophyllum valerinae-tuberosae* the promycelium is 2-celled but there is a single sporidium. The occurrence of a single sporidium is reminiscent of *Monosporidium* discussed under *Aecidium*. Cytological study of *Monosporidium* would undoubtedly reveal whether it is synonymous with *Aecidium* or *Endophyllum*. Barclay did not designate a type for the genus.

Examinations of exsiccati and fixed material of *M. andrachnis* were made, both in free-hand and microtome sections. The pycnia were found to be numerous, epiphyllous, and surrounded by aecidioid telia. Pycnia are subcuticular, conoid, applanate, without noticeable ostiolar paraphyses. The sori are peridiate developing chains of spores. There is no nuclear fusion in the mature spores.

Since in the genus *Endophyllum* the sori are peridiate, and the aecidioid teliospores germinate by 4, 2, or 1 sporidia depending upon the type of nuclear cycle in the species, it was previously considered that *Monosporidium* might be placed with *Endophyllum*. But the finding of the subcuticular pycnia in *Monosporidium* distinguishes it from *Endophyllum* which is characterized by subepidermal pycnia. In this connection the status of the genus *Kulkarniella* recently described by Gokhale and Patel (1951) on *Pavetta tomentosa* from India needs to be considered. The genus *Kulkarniella* was established for an *Endophyllum*-like rust but having subcuticular pycnia instead of subepidermal ones as in *Endophyllum*. The same characters are duplicated in the earlier described *Monosporidium*. Since the actual number of sporidia produced by a germinating teliospore is determined by the type of nuclear cycle and has no generic significance, *Kulkarniella* is treated as a synonym of *Monosporidium*.

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THE IDENTITY OF VIOMYCIN-PRODUCING CULTURES OF STREPTOMYCES

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A comparative study of the morphological and physiological characteristics of *Streptomyces* cultures which produce the antibiotic substance viomycin will be reported in this paper. Certain properties of about forty isolates from soil, together with the organisms known as *S. vinaceus, S. puniceus, S. californicus, S. floridae,* and several strains of *S. griseus* will be considered.

History of the cultures. Numerous viomycin-producing *Streptomyces* cultures studied in our laboratories, and originally regarded as constituting a new species that differed significantly from those described in Bergey's Manual (Breed, Murray, and Hitchens 1948), were designated by the name *S. floridae* (Bartz, Ehrlich, Mold, Penner & Smith 1951). This name was chosen because viomycin was first obtained from the filtrate of a culture (A5014) which had been isolated from soil collected by one of us in Coral Gables, Florida. Although the viomycin-producing cultures were recognized to have much in common with *S. griseus,* as defined by Waksman, Reilly, and Harris (1948), their close resemblance to *S. californicus* was overlooked for two reasons: (1) this species was described as abundantly forming filaments with open spirals—a characteristic not observed in the isolates which produce viomycin, or in *S. griseus;* (2) *S. californicus* was described (Waksman & Curtis 1916, Waksman & Lechevalier 1953) as liquefying gelatin and peptonizing litmus milk slowly—in contrast to rapid proteolysis by the viomycin producers and *S. griseus.*

An isolate which was found to produce an antibiotic called vinactin (Mayer, Crane, DeBoer, Konopka, Marsh & Eisman 1951) was described by Ciba Ltd. (1951) under the name *S. vinaceus.* The description of this species, and the similarity of vinactin to viomycin suggested the possibility of synonymy of *S. vinaceus* and *S. floridae.*

An organism producing viomycin was referred to by Patelski (1950) under the name *S. puniceus,* and described in 1949 by Pfizer (1952). Reexamination of this culture led to the publication of a paper by Routien and Hofmann (1951) concerning their isolate (*S. puniceus*) which was recognized as having many properties of *S. californicus* (Waksman & Curtis) Waksman and Henrici (in Breed, Murray & Hitchens 1948). The ATCC

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organism *S. californicus* 3312, however, differs from the original description of this species by not forming spiral filaments in the aerial mycelium.

Through the cooperation of different investigators, we have now had the opportunity to study isolates of *S. vinaceus, S. puniceus, S. floridae,* and *S. californicus.* Studies on 38 viomycin-producing isolates obtained from soils indicate that the organism is widely distributed in nature. Among the places from which they have been obtained are the following: Fairhope, Alabama; New Haven, Connecticut; Coral Gables, Delray Beach, Homestead, Miami, Florida; Fulton, Missouri; Pittsburgh, Pennsylvania; Clarksville, Tennessee; San Antonio, Texas; LaGrange, Wisconsin; Argentina; Cape Verde Peninsula; Colombia; and Trinidad.

Morphology of viomycin producers. Four characteristics of viomycin-producing strains are obvious in cultures grown on many solid media: (1) red to purple pigmentation developed in the substratal vegetative mycelium and on the underside of mature colonies, but not diffusing into agar; (2) slight gray or light brown coloration of the agar which does not become dark brown or black; (3) aerial mycelium at first white, then turning to gray-green or gray with maturation of the spore masses; and (4) sporophores almost straight, irregularly curved, wavy, branched or unbranched, and sometimes borne in clusters.

Detailed studies were made on the morphology and physiology of a culture of *S. floridae* no. A5014 and eleven other representative isolates carried under the same name, along with similar observations on other isolates obtained from different collections. When grown on agar media conducive to spore formation, aerial hyphae and green-gray to light gray masses of spores generally are produced in abundance. The general appearance of the spore masses suggests relationship to *S. griseus.*

Slide cultures were prepared aseptically for microscopic observations and photographic records. A droplet of suitable nutrient agar, such as medium ASA (table 1), or gelatin was placed upon a slide, inoculated with a small loopful of spore suspension, and covered with a cover slip so as to provide, under a portion of the cover slip, an air space into which the mycelium could grow and form aerial spores. Slide cultures were allowed to incubate in a moist chamber at 25° C. for 5 to 10 days, until characteristic growth and development had occurred. Satisfactory preparations for low power photomicrography were also made by growing cultures on basal nutrient agar containing the mineral salts of Pridham and Gottlieb medium (table 1), and with the carbon source omitted or reduced to 0.2 per cent, in order to limit the amount of growth and facilitate observation of the micromorphology.

Individual substratal hyphae are generally hyaline, branched, and colored purple in the region of dense growth, which occurs at or near the

surface of the agar. The spores are formed basipetally at the tips of branched or unbranched hyphae, or may occasionally be formed in portions of the mycelium which grow in contact with the nutrient gel or glass. Aerial chains of conidia tend to be straight, and chains which mature in contact with the substratum often become curved and irregularly wavy (fig. 1, G, H). Length of the conidial chains varies greatly in our isolates, depending upon conditions of cultivation, but often ranges from about 10 to 85 microns, the usual length being approximately 40 microns. Spores are usually somewhat oval or elongated, their size ranging from 0.7 to 1.6 microns and aver-

TABLE 1. *Composition of different media used for studies on the morphology and physiology of Streptomyces.**

Ingredients	A S A	D T A	G A A	Synthetic	Ca-malate
Agar	2.0	2.0	1.5	1.5	1.5
Asparagine	.....	.....	0.05	.....	.....
Tryptone, Difco	0.5	0.5	.....	.....	.....
NH_4Cl	.....	.....	.....	.....	0.05
$(NH_4)_2SO_4$	.....	.....	.....	0.264	.....
K_2HPO_4	0.3	0.05	0.05	0.565	0.05
KH_2PO_4	.....	.....	.....	0.238	.....
NaCl	0.05	0.05	.....	.....	.....
Ca-malate	.....	.....	.....	.....	1.0
$MgSO_4 \cdot 7H_2O$	.....	.....	.....	0.1	.....
$CuSO_4 \cdot 5H_2O$	0.00064	.....	.....	0.00064	.....
$FeSO_4 \cdot 7H_2O$	0.00011	0.01	.....	0.00011	.....
$MnCl_2 \cdot 4H_2O$	0.00079	.....	.....	0.00079	.....
$ZnSO_4 \cdot 7H_2O$	0.00015	.....	.....	0.00015	.....
Dextrose	.....	1.0	.....	.....	.....
Glycerol	.....	.....	1.0	.....	1.0
Maltose	1.0	.....	.....	.....	.....
Carbon compound as required	.....	.....	.....	1.0	.....
Nitrogen compound as required	.....	.....	.....	= 0.01M nitrogen	.....

* A S A = Anderson's Sporulation Agar Medium
D T A = Dextrose Tryptone Agar Medium
G A A = Glycerol Asparagine Agar Medium
Synthetic = Pridham and Gottlieb (1948) medium.
Amounts are stated in grams per 100 ml. of medium.

aging about 0.8 micron in diameter and 1.3 micron in length. The spores become separated from one another by fragmentation of the chains after about 7 to 10 days.

The photomicrographs presented in this paper were made from living unstained cultures. From the low power photomicrographs (fig. 1, A, B, C, D), it may be seen how similar in micromorphology are *S. vinaceus, S. puniceus, S. floridae,* and *S. californicus.* Numerous observations on these cultures indicate their similarity in both macro- and micromorphology. The culture of *S. californicus* ATCC 3312 is presumed to be a descendent of the original type culture of the species, although it fails to develop spiral aerial

filaments. In addition to having morphological properties in common, all of these isolates peptonize milk rapidly with a final alkaline reaction, and they develop similar pigments on various media. With the exception of ATCC 3312, all isolates liquefy gelatin rapidly and produce viomycin or similar antibiotic compounds.

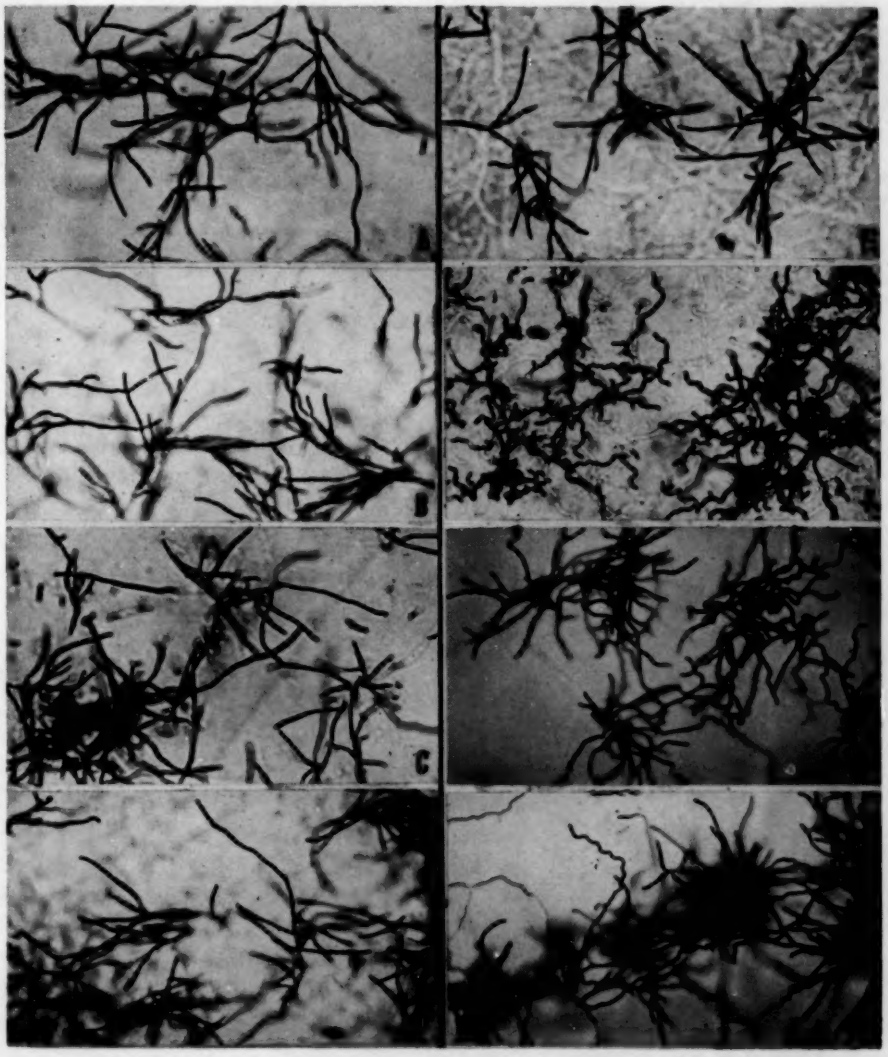

FIG. 1. Photomicrographs of viomycin-producing isolates and related strains of *Streptomyces* (×240); A–D, on starch agar plates; E, F, on dextrose tryptone agar plates; G, H, on maltose tryptone agar micro-slides. A, *S. vinaceus;* B, *S. puniceus;* C, *S. floridae;* D, *S. californicus;* E, *S. griseus* 04727; F, *S. griseus* 1888; G, *S. floridae;* H, *S. californicus.* Note the similarity in irregular branching habit in all, and the tendency to form flexuous filaments in F, G, and H.

Physiological properties of viomycin producers. The studies which were made on physiological activities of the isolates included utilization of various sources of fixed carbon and nitrogen, and certain other tests commonly used in diagnostic bacteriology. Various media were employed in studies of pigment formation. The carbon compounds, used with a synthetic medium (table 1), were dissolved in water and sterilized separately by Seitz filtration, with the exception of inulin, starch, dulcitol, and inositol, which were heat-sterilized directly in the final medium. Approximate amounts of filter-sterilized carbon compounds were added to the autoclaved media in tubes so as to yield a 1 per cent final concentration of each carbon

TABLE 2. *Utilization of carbon compounds by viomycin-producing isolates and related strains of Streptomyces.**

Source Carbon	*S. floridae* Parke, Davis A5014	*S. californicus* ATCC 3312	*S. puniceus* Pfizer 1314–5	*S. vinaceus* NRRL 2285	*S. griseus* Parke, Davis 04727 (streptomycin)	*S. griseus* Waksman 3475 (grisein)
L-Arabinose	0 to ++	± to +	−−	0	0 to +	++++
L-Rhamnose	0	0 to ±	0	±	0	++++
D-Lactose	0 to ++	0 to +	0	0	0 to +++	± to +++
D-Maltose	++++	+ to ++++	−−	++++	++++	+++ to ++++
Sucrose	0 to ±	0 to ±	0	0	0 to ±	0 to ±
D-Raffinose	0	0	0	±	0 to ±	0 to ±
Inulin	0 to ±	0 to ±	0	±	0 to ±	0 to ±
Starch	++++	+++	++++	++++	+++ to ++++	++++
i-Inositol	0	0 to ±	0	±	0 to ±	0 to ±
D-Mannitol	++++	++ to ++++	++++	++++	+++ to ++++	++++
D-Sorbitol	0 to ±	0 to ±	0	±	0 to ±	±

* Symbols:
0 = no growth
± = very slight growth
+ = poor growth
−− = no test made
++ = fair growth
+++ = good growth
++++ = heavy growth

source. Different nitrogen compounds were added to the basal medium, from which $(NH_4)_2SO_4$ was appropriately omitted, so as to provide 0.01 M equivalent nitrogen. Urea and ammonium carbonate were sterilized by Seitz filtration. Heat sterilization was accomplished by autoclaving at 121° C. for 15 minutes. The media were adjusted to pH 6.8 to 6.9. Inoculation was accomplished by transfer of a loopful of spore suspension to each agar slant. Suitable observations were made at intervals during the incubation period of 10 to 14 days at 28° C.

Numerous isolates of *S. floridae* and *S. californicus* ATCC 3312 all utilize D-xylose, D-glucose, D-galactose, D-fructose, cellobiose, D-maltose, D-mannitol, and starch. The consistent responses of numerous individual isolates to different carbon compounds adds further support to the view that these isolates represent the same kind of organism. They grow poorly

on such compounds as L-arabinose, L-rhamnose, D-lactose, sucrose, D-raffinose, dulcitol, i-inositol, and salicin. The isolate A-5014 used the following nitrogen compounds: adenine, xanthine, guanine, β-alanine, DL-alanine, L-arginine, asparagine, aspartic acid, cystine, L-glutamic acid, glycine, histidine, DL-leucine, DL-lysine, DL-phenylalanine, proline, serine, DL-threonine, DL-valine, ammonium carbonate, ammonium sulfate, sodium nitrate, and urea. All isolates of the four named cultures, *S. californicus, S. floridae, S. vinaceus,* and *S. puniceus,* grew satisfactorily on NH_4Cl, $NaNO_3$, or glutamic acid, as well as numerous other compounds supplied as sole sources of nitrogen. All grew poorly on $NaNO_2$, tyrosine, tryptophan, and certain other compounds. Comparative data on the utilization of carbon compounds by viomycin-producing isolates and related strains of *Streptomyces* are shown in table 2.

These isolates of the viomycin-producing group sometimes form a slight brown color in gelatin media, but typical melanin formation, spreading through the agar, was not observed. The striking purple color developed in the mycelium at the surface of the agar is not liberated into the medium in living cultures. The purple pigment can be extracted in aqueous solution and is sensitive to pH, being purple at an alkaline reaction. The purple color disappears upon addition of acid to bring the reaction to pH 3.0, and it is regained by adding alkali again.

Taking into consideration the properties of morphology, pigmentation, and utilization of substrates, it appears that over forty isolates of the viomycin-producing group resemble closely the culture, *S. californicus* ATCC 3312. It is unfortunate that the characteristics of this culture as it now exists do not agree with the description of *S. californicus* by Waksman and Curtis (1916). The original description refers to spiral filaments in the aerial mycelium, whereas the living organism *S. californicus* ATCC 3312 forms straight or wavy filaments, just like the other members of this group.

Comparison of S. californicus and S. griseus. Studies on the comparative morphology and physiology of the viomycin group suggested relationship to members of the species *S. griseus.* Observations on the micromorphology of four purple strains and *S. griseus* (fig. 1) reveal in all strains the presence of branched or unbranched sporophores, sometimes produced in clusters, the chains of spores being straight, wavy or irregularly curved. Since the formation of purple pigment by the substratal mycelium and production of gray-green to gray spores were found to be characteristic of the viomycin producers, a study was made concerning the effects of different culture conditions on formation of pigments in *S. californicus* ATCC 3312 and *S. griseus.* The results of such a study, made for 6 cultures grown on 5 different media, are presented in table 3. The characteristic purple pig-

TABLE 3. *Comparison of the color of aerial and substratal mycelium in viomycin-producing isolates and related strains of Streptomyces grown on five different agar media.**

Agar Medium	Mycelium	*S. floridae* Parke, Davis A5014	*S. californicus* ATCC 3312	*S. puniceus* Pfizer 1314–5	*S. vinaceus* NRRL 2285 (from Ciba)	*S. griseus* Parke, Davis 04727	*S. griseus* Waksman 3475
Glycerol Asparagine	Aerial	White	White	White to light gray-green	White to light gray-green	White to light gray-green	White to light gray-green
	Substratal	White to light gray to slight purple	White to light gray to purple	Purple	White to light gray to slight purple	White to light gray-yellow	White to light yellow
Dextrose Tryptone	Aerial	White to slight gray-pink	Slight growth, white	Light gray-pink to light gray-green	Light gray-pink to slight light gray-green	Light gray-pink to light gray-green	White to gray-pink
	Substratal	Black with slight purple tinge	Gray to slight black	Gray to black	Gray to black	Light gray to red-gray	Light gray-yellow
Starch Synthetic	Aerial	White to light gray-green	White	White to light gray-green	Light gray-green	Light gray-green	Light gray-green
	Substratal	Purple	Light gray to slight purple	Purple	White to light gray to slight purple	Light yellow-gray	Light yellow-gray
Calcium Malate	Aerial	White	White	Light gray-green	White	White to slight light gray-green	White to slight gray-green
	Substratal	White to light yellow	White to light yellow	White	White	Yellow	Gray-yellow to slight light brown
Difco Nutrient	Aerial	White	White	White	White to slight light gray-green	White to slight gray-green	White to slight gray-green
	Substratal	White to slight light yellow	White to slight light yellow	White to light yellow	White to light gray-yellow	Light gray-yellow	Light gray-yellow

* Color comparison with Maerz and Paul, (1950) "Dictionary of Color."
Light gray-green = 11 and 12-B-1
Purple = 46-K-6 to 53-I-11
Pink = 4 and 5-D-1

ment appeared in the substratal mycelium of different isolates of the viomycin group in varying intensity, depending upon the nature of the substrate. The color of substratal growth of isolate A5014 varied from purple when grown on starch agar, to light yellow or white when cultivated on calcium malate or Difco-nutrient agar, to almost black on dextrose tryptone agar. Equally striking was the formation of a red-gray color in the substratal mycelium of several streptomycin-producing strains of *S. griseus*, such as O4727, which suggests a relationship between *S. griseus*, *S. californicus* ATCC 3312, and the viomycin producers. The color of the aerial mycelium and spore masses of *S. griseus* strains, as well as the isolates in the viomycin group, is characteristically gray-green, varying to light gray or almost white in different media. All isolates, for which data are reported in table 3, show light gray-yellow substratal growth on nutrient agar, and red-purple to almost black coloration when grown on dextrose-tryptone agar. The tendency to produce gray-green spore masses on suitable media is shown by both *S. griseus* and the viomycin producers. In the original descriptions of *S. griseus* and *S. griseoflavus* by Krainsky (1914), the gray-green color of the aerial mycelium and spores was emphasized. *S. griseoflavus* was said to differ from *S. griseus* by forming more distinct yellow pigment than the latter when growth in starch NH_4Cl agar or in Ca-malate agar. In our experience with numerous isolates of *S. griseus* and viomycin producers, many gradations of yellow pigment may be observed in Ca-malate medium; hence it seems doubtful whether formation of yellow pigment can be taken as a basis for separation of the species, as was proposed by Krainsky (1914).

Tests for susceptibility to antibiotic inhibition of growth were performed with *S. californicus* ATCC 3312, *S. floridae* Parke, Davis A5014, *S. vinaceus* NRRL 2285, *S. puniceus* Pfizer 1314-5, and *S. griseus* NRRL B1076. Solutions containing 0.1 mg. per filter paper pad, one-half inch in diameter, were applied to surface seeded agar plates. All cultures were resistant to viomycin, cycloheximide, streptothricin, and streptomycin; and all were susceptible to chlortetracycline, oxytetracycline, neomycin, and puromycin.

Susceptibility of these strains to an actinophage was tested with a lytic filtrate prepared from a streptomycin-producing culture of *S. griseus*. While the parent culture and numerous other streptomycin-producing isolates of *S. griseus* were lysed by the phage at dilutions of 10^{-4} or 10^{-5}, among twenty-seven viomycin formers tested with various dilutions of the phage, twenty-two were not susceptible, four were slightly affected, and only strain A5014 showed marked susceptibility. *S. californicus* ATCC 3312 and four grisein-producing strains of *S. griseus* were not susceptible to this phage. It was thus not possible to differentiate the viomycin group from *S. griseus* by means of this actinophage.

Comparisons of the viomycin group with streptomycin- and grisein-producing cultures of *S. griseus* (table 2) show poor growth responses for all on substrates containing sucrose, raffinose, inulin, inositol, and sorbitol, and excellent growth for all on starch and mannitol. The grisein-producing strain of *S. griseus* grew well on arabinose and rhamnose, but all other isolates in table 2 failed to grow on these sources of carbon.

The statements made in regard to carbon utilization by the isolates listed in table 2 are applicable also to twelve isolates of *S. floridae*, twenty streptomycin-producing, and four grisein-producing cultures of *S. griseus*.

In other tests, grisein producers and streptomycin producers show striking differences among isolates of the species *S. griseus*, and some close resemblances are found between isolates of *S. griseus* and the viomycin-producing cultures. Thus, on tyrosine starch agar, certain streptomycin producers formed a dark pigment in the agar, whereas the grisein producers resembled *S. californicus* and *S. floridae* by not forming this pigment. Grisein producers and the viomycin group grew well on $NaNO_3$, but the streptomycin producers utilized this compound poorly.

The various isolates, *S. vinaceus*, *S. floridae*, *S. puniceus*, and *S. californicus* show similarity to *S. griseus* in microscopic morphology of the aerial hyphae and spore chains, and a typical gray-green to gray color of the spore masses. Certain strains of *S. griseus* form pink to red-gray substratal mycelium in dextrose tryptone agar, suggesting a relationship in this respect to typical pigmented cultures of viomycin-producing organisms. Some strains of *S. purpeochromogenus* (Waksman & Curtis 1916) also produce red to purple tinges of color, not very different from the general appearance of viomycin-producing strains.

In view of the well known variation of antibiotic production in *S. griseus*, it would be easy to include the formation of other substances, such as viomycin, in the *S. griseus* repertoire, without changing our concepts of this species. Similarities of substrate utilization, and overlapping of physiological characteristics, would support the view that the various isolates under consideration should be reduced to specific synonymy with the gray-green spore group of *S. griseus*. Furthermore, the formation of a striking purple pigment in the substratal mycelium of *S. californicus* and the viomycin-producers, when cultivated on certain media (table 3), set them apart from the isolates of *S. griseus* which do not produce this pigment. It is proposed that the purple viomycin-producing group and related cultures, such as ATCC 3312, not forming spirals, should be recognized as variety *purpureus*, belonging in *S. griseus*. All strains of this species have in common gray-green spore masses and aerial mycelium which is branched, straight, or wavy, with a tendency to form tufts, occasional loops, but no true spirals. Thus the nomenclature is simplified by reducing *S. floridae*, *S. vinaceus*,

S. puniceus, and *S. californicus* ATCC 3312 to synonymy in the new variety *purpureus*. The transfer of these organisms to a variety of *S. griseus* reduces the number of species names, gives emphasis to morphological criteria of speciation, and serves as an example of a desirable trend toward "lumping" rather than "splitting."

Diagnosis. *Streptomyces griseus* (Krainsky) Waksman and Henrici var. **purpureus** var. nov. The new variety designates strains of *S. griseus* that form a purple color in the substratal mycelium on many media. Several strains produce the antibiotic, viomycin, under suitable conditions.

Synonyms. *S. vinaceus* Ciba (1951), *S. puniceus* Patelski (1950), *S. floridae* Bartz et al. (1951), *S. californicus* sensu Routien & Hofmann (1951) sed non (Waksm. & Curtis) Waksm. & Henrici (1916, 1948).

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BULLETIN OF THE TORREY BOTANICAL CLUB
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CHROMOSOME STUDIES OF PLANTS FROM THE ARCTIC SLOPE OF ALASKA. I. RANUNCULACEAE[1]

F. H. BORMANN AND A. V. BEATTY

During the summer of 1953 the first author was a member of the Boston University Physical Research Laboratory Expedition[2] to northern Alaska. In addition to performing regular vegetational survey duties for the expedition, there was an opportunity to collect meristematic material from a number of flowering plants growing in the lower foothill and coastal plain area of the central portion of the Arctic slope of Alaska. Ninety-seven such collections were made. Chromosome studies are being made by the second author. This survey should contribute to a clearer understanding of the Arctic flora and the chromosomal morphology of certain groups.

An attempt was made to collect all meristematic material from single plants; whenever this proved impossible, collections were made from two or more plants growing within a few feet of each other. Root tips, flower buds, and/or young leaves were removed and with the collection number of the plant(s) from which they were taken were placed in a small vial containing a solution of 25% glacial acetic acid and 75% isopropyl alcohol. A description of the habitat was recorded for each collection, and the plants were later pressed and dried.

The vials of preserved material were sent by airmail to the coauthor at Emory University. A small portion of the material in each vial was saved for acetocarmine studies, while the remainder was placed in a Craf fixative, subsequently embedded in paraffin, sectioned and stained with Heidenhain's iron alum hematoxylin.

The pressed specimens were sent to specialists in Arctic flora for exact determinations. They were given herbarium numbers and are now in various herbaria.

As the chromosome studies are completed, the following information will be published by families: verified specific names; chromosome counts and any other observable nuclear phenomena; habitat description and place of collection; herbarium numbers of the plants from which the meristematic material was taken; and the name and location of the herbarium.

The authors are indebted to Dr. A. E. Porsild of the National Museum

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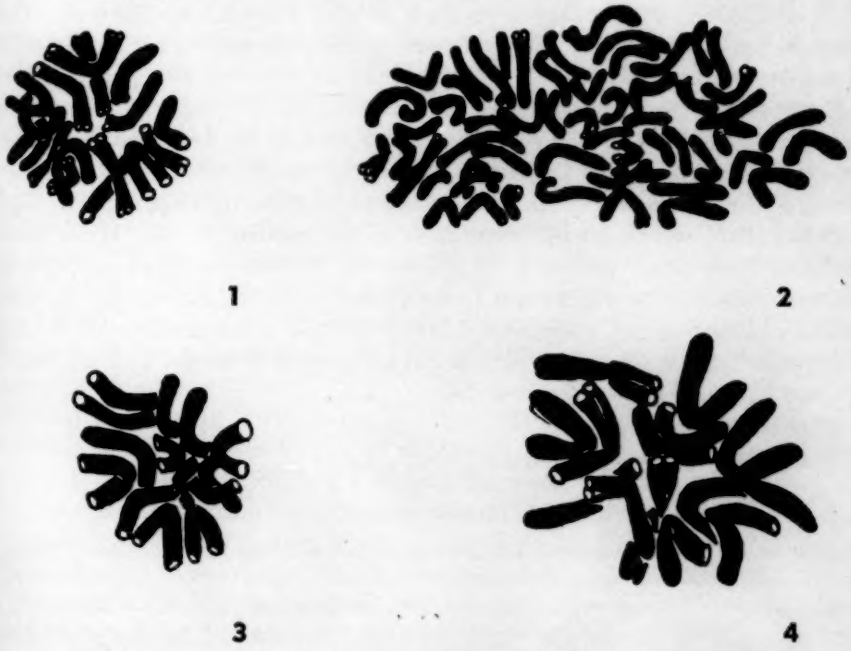
[2] Under contract with the U.S.A.F., Wright Air Development Center (Contract AF33-038-15615); there is no objection to publication on grounds of military security.

of Canada for identifying the plants mentioned in this paper. The herbarium numbers following each plant are those of the Canadian National Herbarium at Ottawa. Duplicate specimens of all collections with the exception of *Caltha palustris* L. var. *Arctica* (R. Br.) Huth. (C.N.H. 225517) and *Ranunculus lapponicus* L. (C.N.H. 225521) are at present in the Emory University Herbarium.

Two collections of *Ranunculus lapponicus* L. were made. The first (C.N.H. 225522) was collected on June 24 in a wet lowland underlain by peaty soil near old Umiat. The second (C.N.H. 225521) was gathered in a lowland sphagnum-birch-heath community near Umiat. In both collections



FIGS. 1–4. Camera lucida drawings of somatic mitoses. All magnifications are × 2800. FIG. 1. *Pulsatilla ludoviciana*, 2N—16. FIG. 2. *Caltha palustris* var. *Arctica*, 2N—56. FIG. 3. *Anemone parviflora*, 2N—14. FIG. 4. *Anemone richardsonii*, 2N—14.

chromosome counts made from root tip material revealed a 2N number of 16. This agrees with the reports made previously by Langlet (1932) and Flovik (1936).

One collection of *Pulsatilla ludoviciana* (Nutt) Heller (C.N.H. 225520) was made on June 16 from plants growing on the dry slope of a ridge west of Umiat Mountain. A 2N count of 16, made from sectioned leaf bud material, is the first report of a chromosome number for this species. Langlet (1932) previously reported two species of *Pulsatilla* having 2N counts of 16 and one with a 2N count of 32.

A single collection of *Caltha palustris* L. var. *Arctica* (R. Br.) Huth. (C.N.H. 225517) was made on June 16 in a valley three miles west of Umiat Mountain. The plant was taken from the silty soil of a grassy swale beside a beaded stream. Studies of root tip and bud material showed a 2N number of 56. Langlet (1927, 1932, 1936) and Gregory (1941) have reported a 2N number of 32 for *Caltha palustris* L., while Langlet has published for other varieties of this species 2N numbers of 56, 58, 58–59, and 60. The report given here of 56 was possible only after examination of several hundred somatic metaphases to find one in which a reliable count could be made.

Anemone parviflora Michx. (C.N.H. 225515) and *A. richardsonii* Hook (C.N.H. 225516) were collected on June 15 and June 22, respectively. The first was found growing in relatively dry, black, silty soil on a ridge west of Umiat Mountain; while the second was discovered in the wet, peaty soil of a disturbed lowland area near old Umiat. Root tip material was examined and the 2N number of chromosomes was found to be 14 in both species. This is the first report of a chromosome number in *A. richardsonii*. Langlet (1932), using material from the botanical garden in Copenhagen, and Moffett (1932) working with material from the garden of John Innes Horticultural Institute reported a 2N number of 16 for *Anemone parviflora*. Reports of 2N numbers of 14 and 16 have been published for another species of this genus. Sugiura (Gregory, 1941) reported a 2N number of 16 for *A. hepatica* var. *acuta*, when all other reports on this species and its varieties had been given previously as 14.

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A CYTOTAXONOMIC STUDY OF BOUTELOUA CURTIPENDULA AND B. UNIFLORA

L. ERNEST FRETER AND WALTER V. BROWN

The importance of *Bouteloua curtipendula* (Michx.) Torr. is evident from the number of commercial strains and from a statement in the Forest Service Range Plant Handbook (1937) that it is thought by many that this species is the most promising of the grama grasses for domestication. It produces fairly nutritious, palatable forage and, when seeded alone or in mixtures, can be used for both forage and reclamation purposes (Harlan 1949). Its drought resistant characteristics contribute to its value, especially in the Southwest. Very little is known, however, concerning the range value or use of the closely related species, *B. uniflora* Vasey. Undoubtedly it has some importance because of its apparent drought resistance, but its rather restricted range to south central Texas and north central Mexico may limit its value. The distribution and taxonomy of these two species have not been understood well in the past (compare I. M. Johnston 1943, and L. H. Shinners 1954). The purpose of the present investigation is to evaluate the relationship between these two taxa, using evidence from their distribution, morphology and cytology.

Distribution. In their range of ecological adaptation and distribution these taxa differ markedly. *B. curtipendula* is a very widespread species, being found on hills, plains, and prairies from Southern Canada to Argentina. *B. uniflora*, on the other hand, is found on and along the limestone hills of the Texas Edwards Plateau and south into the Mexican states of Coahuila and Nuevo Leon. The distribution map of *B. uniflora* (fig. 1) was compiled from collections and observations made in the field by the authors, and from specimens obtained from the Gray Herbarium of Harvard University, the National Herbarium of the Smithsonian Institution, the Tracy Herbarium of Texas A. and M. College, the Herbarium of the Missouri Botanical Gardens, and the University of Texas Herbarium. Grateful acknowledgment is made to the curators of the herbaria cited for their coöperation in making specimens available.

Morphology. Vasey (1891) first described *B. uniflora* as a distinct species. His description was based upon material from Crockett County, Texas, collected by G. C. Nealley. The name, *B. uniflora*, is based upon the occurrence in each spike of one perfect spikelet, but variation in this character has led to confusion in the correct identification of both *B. uniflora* and *B. curtipendula* specimens. Vasey (1891) and Scribner (1900) limited *B. uniflora* to forms which had, among other characters, spikes composed of one

perfect spikelet. Silveus (1933), however, observed in inflorescences of *B. uniflora* the occasional occurrence of spikes with 2 or 3 typical curtipendula-like spikelets. These spikes are usually intermediate in form. Hitchcock (1950) also recognized this condition in *B. uniflora,* spikes with more than one spikelet, and applied *B. uniflora* to forms which had, other characters taken into consideration, 1 or 2 spikelets per spike. The spike of *B. uniflora* in its usual condition does bear a single perfect spikelet, although a few basal spikes on the inflorescence may occasionally bear more than one spikelet.

FIG. 1. Distribution map of *B. uniflora.* Each dot represents an area in which one or more specimens of this species have been collected.

Spikes of *B. curtipendula* usually bear many spikelets, although this species is extremely variable as compared with *B. uniflora.* Notwithstanding the occasional occurrence of curtipendula-like spikes on *B. uniflora* plants (Silveus 1933) and uniflora-like spikes in the inflorescences of some *B. curtipendula* plants, there is still no great difficulty in distinguishing between these species. The separation, for the majority of specimens, is based upon differences in gross morphology. *B. curtipendula* is a stouter and usually a

much larger plant than is *B. uniflora*. Furthermore, *B. curtipendula* is much more rhizomatous and much less stoloniferous than is *B. uniflora*.

Within the range of variability in *B. curtipendula* may be found plants which closely approach the *B. uniflora* aspect. The variability within *B. curtipendula* has caused most of the difficulty in distinguishing between these taxa. However, these plants of *B. curtipendula* which approach the aspect of *B. uniflora* do not present a regular distribution pattern in either Texas or Mexico. They are widely scattered. Furthermore, where the ranges of *B. uniflora* and *B. curtipendula* coincide, these plants of *B. curtipendula* which approach the *B. uniflora* condition are not found more often than in those areas in which coincidence of ranges does not occur.

Some plants of *B. uniflora* found in western Coahuila, Mexico, exhibit tendencies toward smaller size of all parts. A specimen of *B. uniflora* (I. M. Johnston, 9060, Gray Herbarium) from western Coahuila shows this tendency toward smaller size, but still compares favorably with the probable type or isotype of *B. uniflora* (deposited Gray Herbarium). Some characters of Mexican *B. uniflora* plants, such as spikelet length or glume length, approach those of *B. curtipendula;* however, this should not be interpreted as an intergradation of characters because the tendency toward decreased size is clearly a morphologic expression away from the general aspect of *B. curtipendula*. In separating plants of *B. uniflora* from plants of *B. curtipendula* which approach the aspect of *B. uniflora*, it is necessary to take into consideration several comparative characters and not just a few (table 1). The table of comparative characters has been arranged so that the most stable points of comparison precede those of lesser stability. These characters remained constant and fixed in plants of these taxa and their progenies, when grown under the same conditions in experimental field plots.

Cytology. A cytological investigation concerned primarily with meiosis in microsporocytes was undertaken in order to determine chromosome numbers and to characterize the meiotic process of the two species. And furthermore, the ecological and morphological differences between *B. uniflora* and *B. curtipendula* were correlated with the cytological evidence.

Materials and methods. Inflorescences were killed and fixed in either 3:1 absolute-acetic or absolute-proprionic acid and stored in 70% ethyl alcohol until used. Smears from squashed anthers were stained with either acetocarmin or proprionocarmin; the propionocarmin usually gave better contrast. Pollen stainability with cotton blue in lactophenol was taken as an index of pollen viability. When inflorescences were unavailable, root tip smears were made from material of *B. uniflora, B. radicosa* (Fourn.) Griffiths, and *B. chondrosioides* (H. B. K.) Benth. ex S. Wats. The latter two species were investigated in order to provide additional information concerning the basic chromosome number within the section ATHEROPOGON.

The root tips were pretreated with 8-hydroxyquinoline according to the method of Tjio and Levan (1950); the smears were stained with aceto-orcein.

Twelve *B. uniflora* plants, collected on the Edwards Plateau northwest of San Antonio, Texas, were investigated cytologically. Seven of these plants were used for the meiotic study; these were collected from the following counties: southwest Sutton, northwest Edwards, northern Edwards, northeast Kerr (2 plants 3 miles apart), and northwest Kendall (2 plants from

TABLE 1. *A comparison of B. uniflora and B. curtipendula*

Character	*B. uniflora*	*B. curtipendula*
Rachis of the spike	An extended green awn, longer than first glume.	Rarely awn-like, if so, shorter than first glume.
Composition of the spike	Usually 1-spikeleted spikes. Rarely 2 or 3 basal spikes present bearing more than 1 spikelet.	Commonly, 3–13 spikeleted spikes. Spikes rarely with 1 spikelet; if so, 3-many basal spikes present bearing more than 2 spikelets.
Lemma	Entire, rarely minutely 3-toothed.	Usually 3 short awns present.
Culm	Slender, usually 4.5 to 6 dm. in height.	Stouter, usually 6 to 9 dm. in height.
Rudiment	Usually a single hispid awn.	Usually a minute short awned scale with rudimentary palea or a 3-awned lemma.
Spikelet length	Usually 7–8 mm. long.	Usually 5–8 mm. long.
Anther color	Always yellow.	Yellow, orange, red.
First glume	Glume usually 1 mm. wide and 3 mm. long; widest near middle.	Glume usually 0.8 mm. wide and 5 mm. long; widest near base.
Rhizome	Rarely rhizomatous.	Stout and coarse rhizomes.
Stolon	Usually stoloniferous.	Rarely stoloniferous.
Leaf blade	Usually 2 mm. wide.	Usually 3–4 mm. wide and more basally arranged.
Mature inflorescence length.	1–1.5 dm.	1.5–3 dm.

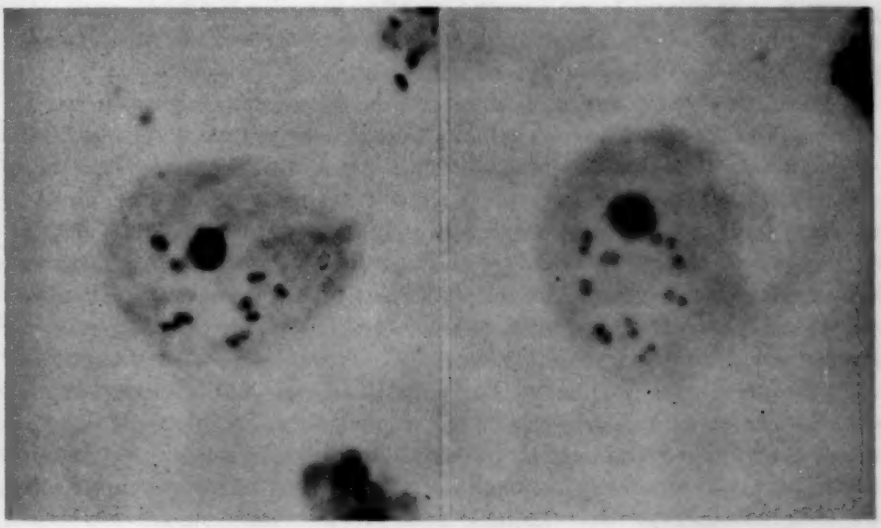
the same location). The other five plants were used in the mitotic investigation of *B. uniflora* and were collected from Kendall County (3 plants) and Kerr County (2 plants).

Five plants of *B. radicosa* used for root tip material were grown from seed obtained from the U.S.D.A. Soil Conservation Service, accession #A 14240, collected at the Tucson Nursery, Arizona, for which acknowledgment is made to E. G. Hendricks. One plant of *B. chondrosioides* collected in Jeff Davis County, Texas, was investigated for its chromosome number.

Meiosis was studied in fifteen plants of *B. curtipendula* collected from the following Texas counties: east central Crockett, west central Sutton,

northeast Brewster, northeast Irion, central Kerr (2 plants from different locations), southern Val Verde (2 plants from different locations), central Travis (4 plants from one location and 1 from another), western Travis, and central Victoria. Additional studies were made on six plants which were grown from seed obtained from the U.S.D.A. Soil Conservation Service, accession #T-15, 241(50)G, collected at Dalhart, Texas. Voucher specimens for most of the collections used in this investigation have been deposited in the University of Texas Herbarium.

Observations. Mitosis in *B. uniflora* is regular. At metaphase 20 chromosomes were always observed; during anaphase the 40 chromatids separated with 20 passing to each pole. Meiosis in *B. uniflora* anthers is also regular; no abnormalities were noted. During diakinesis 10 bivalents were always apparent (figs. 2 and 3), pairing was complete; the homologues of each biva-



FIGS. 2 and 3. Photomicrographs of diakinesis in microsporocytes of *B. uniflora* showing ten bivalents.

lent separated regularly and passed to opposite poles in anaphase I. During division II, anaphase was regular with the 20 chromatids in each cell separating, 10 passing to each pole forming a tetrad of $n = 10$ microspores equal in size. All plants of *B. uniflora* examined had a chromosome number of $2n = 20$. Pollen stainability in plants of this species was excellent.

In contrast with the regular type of microsporocyte division in *B. uniflora*, the division in *B. curtipendula* is marked by considerable plant to plant variation. Depending upon the type of division found in ALL OF THE MICROSPOROCYTES OF AN ANTHER SAC, all plants investigated should be placed conveniently into one of three groups. To group 1 belong these plants in which the meiotic division appeared regular for ALL MICROSPOROCYTES IN

THE ANTHER. This group was composed of the following plants: east central Crockett ($2n = 52$), central Victoria ($2n = 40$), central Travis ($2n = 40$), and four plants grown from the seed obtained from the U.S.D.A. ($2n = 40$ for the four). At diakinesis complete pairing was evident. No multivalents were observed in any of the $2n = 40$ plants. During anaphase I the homologues of bivalents separated and migrated to opposite poles. At anaphase II the chromatids separated, passed to the poles, and four microspores equal in size were eventually formed. Pollen from these plants stained well.

Plants of group 2 are characterized by a low degree of chromosomal pairing in ALL THE MICROSPOROCYTES OF AN ANTHER during division I. This group was composed of the following plants: western Travis, northeast Irion ($2n = 86$), central Kerr (2 plants from different locations), central Travis (4 plants from one location, $2n = 86$ for all), southern Val Verde (2 plants from different locations, one was $2n = 82$, no reliable count for the other), and two plants grown from seed obtained from the U.S.D.A. source mentioned earlier ($2n = 80$, $2n = 96$). In this group, division I may proceed in ONE OF TWO WAYS AMONG DIFFERENT MICROSPOROCYTES IN THE SAME ANTHER SAC. The more common method was characterized by an unequal division with an asymmetric anaphase I figure. About 10 chromosomes passed to one pole; about 76 remained in place at the other pole; that is, the spindle is essentially unipolar. Presumably, the smaller group of chromosomes represented homologues of bivalents, (Harlan 1949). The sister cells formed by this division were unequal in size, the smaller having the fewer chromosomes. Anaphase II was usually regular with the chromatids of each cell separating and passing to opposite poles. Tetrads composed of two small and two larger cells were most common, although pentads and hexads were occasionally seen. Harlan (1949) has reported octads. Each of the two larger cells was reduced only by the number of bivalents originally present; each of the two smaller cells contained a number of chromosomes equal to the number of bivalents originally present. The less common method of division I within this group was peculiar in that a spindle was formed but no actual chromosome separation took place at this time, although cytokinesis occurred. This "division" produced two cells, one having a nucleus and the other without a nucleus. Usually, but not always, the anucleate cell "divided" again. The nucleate cell then divided. The result of the entire division was either a triad or a tetrad with only two cells possessing nuclei. The larger pollen grains in plants of this group stained well, the smaller ones less so.

To group 3 belong those plants which show a considerable range in degree of chromosomal pairing among DIFFERENT MICROSPOROCYTES OF THE SAME ANTHER SAC. Group 3 was composed of plants from west central Sutton ($2n = 74$) and northeast Brewster ($2n = 80$). During division I, some microsporocytes showed no pairing, others showed a degree of pairing compar-

able to that in group 2, and in others, although less common, pairing was apparently complete. All of these types could be found within the same anther sac. If no pairing occurred, the product of the entire division would be a diad; if a low degree of pairing was the case, tetrads, pentads and hexads as in group 2 would be elaborated. If complete pairing was approached, a tetrad as in group 1 would be formed. The larger pollen grains from this group stained well; the smaller pollen grains, especially those derived from polyads, usually did not.

Reproductive behavior. Seed set measured by observations of individual caryopses in *B. uniflora* spikelets was on an average 16%; however, the plant to plant spread was 9% to 22%. Germination measured by growing the seeds in pots to the early seedling stage (under greenhouse conditions) was 61%. Progeny tests in experimental field plots indicated that *B. uniflora* reproduces sexually, (based upon the presence of variation within the progeny). In the group 1 plants of *B. curtipendula* both percentage seed set and the percentage germination were highly variable. Progeny tests indicate sexual reproduction for this group; size characters of *B. uniflora* could be found in the progeny of some of these plants. *B. curtipendula* plants of group 2 usually had a high value for both seed set and germination. Progeny tests indicated that these plants are apomictic. According to Bryant (1952), the apomictic mechanism is characterized by an unequal division I of the megasporocyte similar to that of the microsporocyte. The four megaspores eventually disintegrated; an enlarging nucellar cell formed an 8-nucleate embryo sac; the egg cell enlarged, divided, and eventually formed the aposporic embryo. Evidence gained by emasculating inflorescences indicated that these plants are pseudogamous. Plants of *B. curtipendula* in group 3 were equal to plants of group 2 in both seed set and germination values. These plants appeared to be apomictic by progeny tests. Pseudogamy was also indicated for this group. The reproductive behavior, distributional, morphological, and cytological evidence, therefore, support the interpretation that *B. uniflora* and *B. curtipendula* are distinct species.

Depending upon certain associated morphological characters, one can usually separate plants of *B. curtipendula* belonging to group 1 from those plants belonging to either group 2 or group 3. It is apparent that there is some correlation between meiosis and morphological expression in these plants. Plants having the following characters usually belong to group 1: coarse, basally arranged, blue-green leaves; late flowering; susceptibility to rust; and extensive rhizome systems. Plants of either group 2 or group 3 usually have the following associated characters: fine, yellow-green leaves; fine stems; early flowering; less susceptibility to rust; and a tendency toward being more stoloniferous and less rhizomatous than those plants of group 1. These character associations agree substantially with those reported by Harlan (1950).

Discussion. In evaluating the significance of the cytological data, the other species in the section ATHEROPOGON should also be considered. The investigations of Fults (1942) and Brown (1950), indicated that the basic chromosome number for the section ATHEROPOGON was $x = 7$. There is a growing body of evidence in the literature, however, which indicates that the basic number is $x = 10$. Snyder and Harlan (1953), reported $2n = 40$ for five sexual strains of *B. curtipendula*, $2n = 20$, 21, 22 for some plants of *B. filiformis* and $2n = 20$ in Puerto Rican material of *B. heterostega*. Observations made by the authors of $2n = 20$ in Texas material of *B. uniflora*, of $2n = 40$ in six plants of *B. curtipendula*, of $2n = 20$ for five plants of *B. radicosa*, and of $2n = 20$ for one plant of *B. chondrosioides* further support the assumption that $x = 10$ in the section ATHEROPOGON. Snyder and Harlan (1953), further present evidence for and conclude that the basic chromosome number for the section CHONDROSIUM and for the whole genus, *Bouteloua*, is $x = 10$. The evidence for $x = 10$ in *Bouteloua* supports the assumption that plants of *B. curtipendula* having $2n = 40$ are tetraploids. Counts lower than 40 have been reported (Fults 1942). If $x = 10$, these would represent aneuploids. No diploid plants of *B. curtipendula* have been reported.

In the light of present information, *B. uniflora* appears to be a primitive diploid species having a very restricted distribution while *B. curtipendula* represents a polymorphic, polyploid complex of wide distribution. In discussing the origin of this polyploid complex, the origin of the tetraploid must first be considered. Autopolyploidy from either *B. uniflora* or a diploid *B. curtipendula* apparently is not the most probable explanation for the origin of tetraploid *B. curtipendula* plants. This is attested to by the following observations: The morphological variation between *B. curtipendula* and *B. uniflora* was discontinuous; during diakinesis no multivalents were seen in these tetraploids; complete pairing of the homologues was evident. Furthermore, seed fertility in these tetraploid *B. curtipendula* plants was usually greater than in the plants of *B. uniflora*. In addition to this, four *B. curtipendula* plants with high chromosome numbers ($2n = 86$) were morphologically similar to *B. uniflora*, although other characters were discontinuous, while other *B. curtipendula* plants (Harlan's Tucson strain, 1949) with higher chromosome numbers than $2n = 86$ do not approach the *B. uniflora* aspect.

A more plausible hypothesis for the origin of tetraploid *B. curtipendula* plants would be that they arose through either allopolyploidy or segmental-allopolyploidy (as defined by Stebbins 1950) with *B. uniflora* and another related diploid species as ancestral parents. If *B. curtipendula* arose through segmental-allopolyploidy, selection favored the further differentiation of structural differences between the chromosome sets of the two genomes so that eventually there resulted a stable segmental-allopolyploid

which formed only bivalents during meiosis. Selection pressure would have made it in effect an allopolyploid. On the other hand, if there existed only small structural differences between all of the chromosomes in the two genomes, selection would have favored the loss of these differences so that eventually an autopolyploid condition would have arisen. That this latter type of evolution occurred does not seem too probable since no multivalents were observed in tetraploid material of *B. curtipendula*.

If the hypothesis of an allopolyploid or segmental-allopolyploid origin of tetraploid *B. curtipendula* plants is valid, there are some suggestions that *B. radicosa*-like plants may have been involved in this together with plants of *B. uniflora*. *B. curtipendula*, especially the sexual plants, has many characters which are intermediate between those of *B. uniflora* and *B. radicosa*. *B. radicosa* occurs within the range of *B. uniflora* (Hitchcock 1913). *B. uniflora*, *B. curtipendula*, and *B. radicosa* are all found in the state of Coahuila, Mexico (Johnston 1943). Generally, one would expect the progeny of an allopolyploid to be intermediate between the parental species; however, one would also expect a small percentage of the progeny in later generations to show characters unlike those of the original parents. Some progeny of tetraploid *B. curtipendula* plants show a tendency toward certain characters associated with *B. uniflora*, and others show a tendency toward other characters associated with a *B. radicosa*-like plant.

In explaining the polyploid complex of *B. curtipendula*, the hypothesis of the segmental-allopolyploid origin of the tetraploid is more reasonable in that varying degrees of auto- and allopolyploidy above the tetraploid level could then become manifest, depending upon the original constitution of the individual chromosomes of the two genomes. The polymorphic attributes of the complex could be accounted for by assuming somatic mutation and chromosomal segregation since the tetraploid became established.

SUMMARY

1. *B. uniflora* appears to be a rather restricted species, being found on and along the limestone hills of the Texas Edwards Plateau and south into the Mexican states of Coahuila and Nuevo Leon. *B. curtipendula*, on the other hand, is quite widespread, being found on hills, plains, and prairies from southern Canada to Argentina. From the evidence of distribution, morphology, and cytology, *B. uniflora* and *B. curtipendula* appear to be "good" species. The diagnostic characters of the two taxa have been tabulated.

2. Meiosis in anthers of *B. uniflora* is regular whereas in *B. curtipendula* meiosis in microsporogenesis may be regular, or variably irregular. The basic chromosome number for *B. uniflora* and *B. curtipendula* seems to be $x = 10$; *B. uniflora* being a diploid species and *B. curtipendula* showing varying degrees of polyploidy. Additional evidence from *B. chondrosioides* and *B. radicosa* together with investigations of other workers supports the previous assumption that $x = 10$ for the section ATHEROPOGON.

3. The authors have postulated that at least two species have been involved in the formation of tetraploid *B. curtipendula* plants. The mechanism by which this occurred is assumed to be segmental-alloploidy. *B. curtipendula* has a morphologic expression intermediate between that of *B. uniflora* and some putative *B. radicosa*-like taxon. Above the tetraploid level, varying degrees of allo- and autopolyploidy have arisen, producing a polyploid complex with apomixis.

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BULLETIN OF THE TORREY BOTANICAL CLUB

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AN UNDESCRIBED MESQUITE RUST[1]

FREDERICK W. BIEBERDORF, ROY B. MEFFERD, JR. & CYRIL W. BLACKMON

Two species of rust infecting mesquite, *Prosopis juliflora,* have been described previously, *Ravenelia arizonica,* and *R. holwayi* (Arthur 1934). The latter is common in Texas. In addition, the trees in this area are almost universally infected with an autoecious, macrocyclic rust which we have named *Puccinia prosopidis* (fig. 1). Infected trees exhibit a marked ability to survive infections of even gross proportions and many are simultaneously infected with this species and *R. holwayi.* There is considerable variability in the relative proportions of the two species evident in different seasons. In the summer of 1953 very little *R. holwayi* was to be found, while trees were almost universally heavily infected with *P. prosopidis* for an area of about 200 miles around San Antonio. This summer, 1954, very little *P. prosopidis* was evident and *R. holwayi* infection predominated. The rainfall of both summers was subnormal, and the only readily evident difference in the two seasons was the presence of several heavy dust storms in the late spring of 1954. Dust clouds were blown in from West and North Texas. These areas are heavily infested with Mesquite, and spores of *R. holwayi* undoubtedly accompanied the dust. The rust seems to be very well adjusted parasitically to the tree so that it does not destroy its sustenance, but it does induce a marked hypertrophy around the sori.

Puccinia prosopidis, sp. nov. Spermagoniis amphigenis, dispersis, subepidermicalibus, lageniformibus elevatisque, 50–60 μ altis, erumpentibus, punctiformibus, 40–50 μ in diam., paraphysibus non visis, hyphis recipientibus tenuibus, flexuosis; spermatiis 1.9 μ in diam., aeciis et urediis praecedentibus vel associatis; aeciis uredinoideis, amphigenis, rubro-brunneis; aeciosporis irregularibus, angularibus, ad apicem rotundatis vel ellipsoideis, inferne attenuatis usque truncatis, subtiliter verruculosis; urediis amphigenis fusco-cinnamomeis, soris compactis confertisque, majoribus tortuosis et crispatis, petiolos, folia vel amenta hypertrophientibus, soris singulis 0.5–1.5 mm. longis, 0.2–0.3 mm. latis, 50–150 μ altis, in greges usque 7.5 × 2.0 cm. confluentibus, epidermide lateraliter rumpenti et soros detegenti, eroso, laminationes convolutas longitudinales efformanti, paraphysibus nullis; urediosporis irregularibus, clavato-oblongis, 15–20 × 35–40 μ, membrana fusco-rufobrunnea, 1.5–3.0 μ crassa, ad apicem incrassata, minute et uniformiter verruculosa, poris 6 praedita, pedicello sporae aequanti, 2–4-cellulari; teliis urediis conformibus sed obscurioribus et purpurascentibus; teliosporis bicellularibus, ovatis, cellulis globosis et aequalibus, ad septum constrictis,

[1] The authors wish to thank Sister Mary Clare Metz of Our Lady of the Lake College, San Antonio, for making the Latin description.

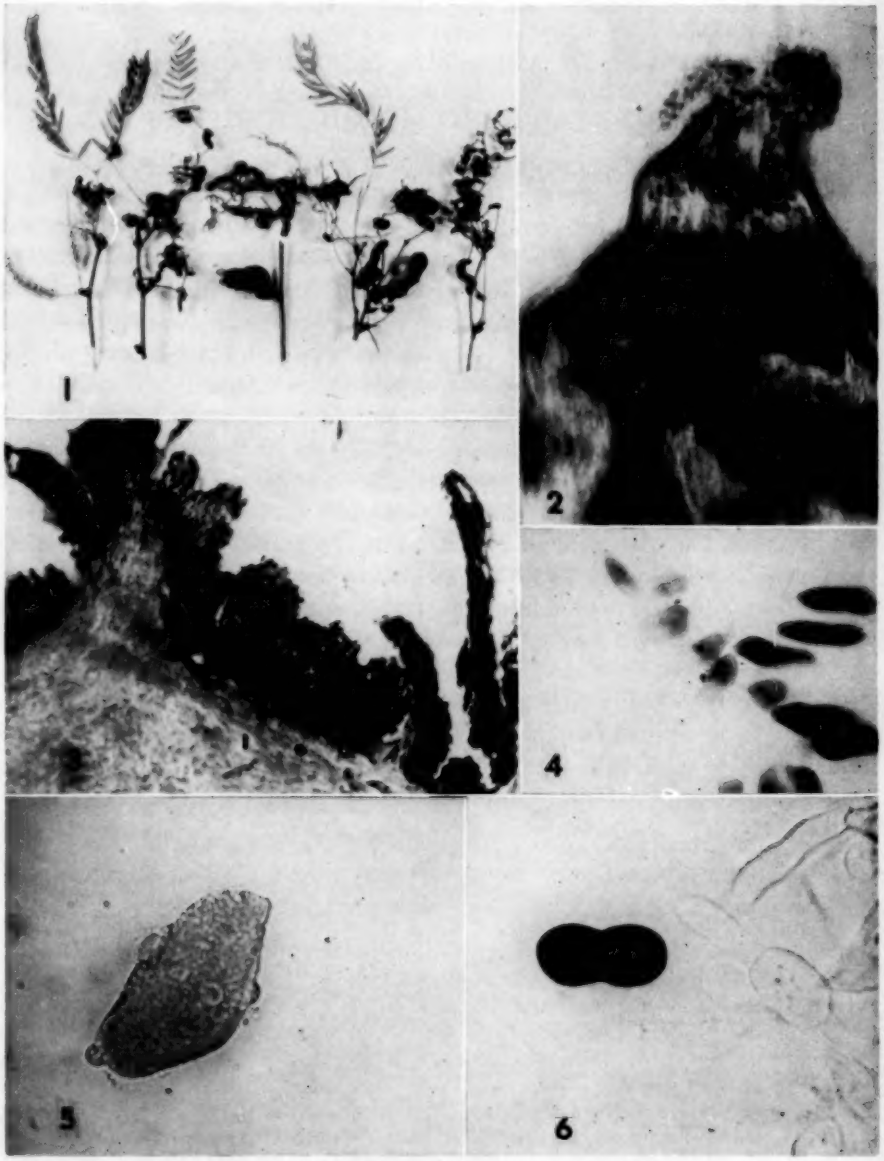

FIG. 1. Rust Galls on Mesquite. Galls occur on stems, petioles, leaflets and the inflorescence. Leaflets approximately 5 inches in length. FIG. 2. Mature pycnium extruding pycniospores. Receptive hyphae may be observed within the structure. Section from small pustule taken from petiole. ×44; stain, Heidenhain's iron hematoxylin. FIG. 3. Uredia. Cross-section of rust gall. Uredia are uredionid, dark cinnamon brown, compact and crowded. No paraphyses or peridia are seen. Spore pedicels are composed of from 2–4 cells. ×100. FIG. 4. Urediospores, showing irregular shapes and immature forms. ×440; stain, Heidenhain's iron hematoxylin. FIG. 5. Urediospore showing equilateral pores and verrucose surface. ×970. FIG. 6. Two-celled teliospore showing surface sculpturing. ×970.

10–15 × 25–34 μ, membrana cacaina, 1.0–1.5 μ crassa, uniformi, continua, glabra, poris ad septum et apicem, pedicello brevi, fragili, deciduo; promycelio teliosporarum germinantium septato, basidiosporis sessilibus, sphaericalibus, 10–15 μ in diam. hyalinis, fragilibus, glabris. Hospes, Prosopis juliflora; locus, Texas.

Spermagonia amphigenous, scattered, sub-epidermal, flask-shaped and raised (50 to 60 μ), erumpent, punctiform, diameter 40–50 μ, paraphyses not seen, receptive hyphae slender and flexuous; spermatia average 1.9 μ in diameter; precede or accompany aecia and uredia (fig. 2). Aecia uredinoid, amphigenous, reddish-brown, caeomoid; aeciospores irregular in shape, angular, rounded to ellipsoid apically, pinched to truncate distally, 15–20 μ by 18–22 μ; wall tan, 1 μ thick, thinned distally, finely verrucose. Uredia uredinoid, amphigenous, dark cinnamon-brown, sori compact and crowded, becoming very large, tortuous and curled, causing considerable hypertrophy of petioles, leaves, or catkins. Individual sori range from 0.5 to 1.5 mm. in length, 0.2 to 0.3 mm. across and 50–150 μ deep, (fig. 3). Complete soral aggregates may be up to 7.5 cm. long and 2.0 cm. across.

The epidermis breaks laterally and sori become naked early. Epidermis on large sori erect and erose, evident as narrow convoluted lamellations generally extending considerable distances lengthwise so as to give the sori a lined appearance. No paraphyses. Urediospores irregular (fig. 4) clavate-oblong, 15–20 μ by 35–40 μ; wall dark reddish brown, 1.5 to 3.0 μ thick, thickened at apex, closely, finely and evenly verrucose, 6 pores equilateral (fig. 5). Borne on single pedicels of about the same size as the spore with 2–4 cells in pedicel.

Telia like uredia, but darker with a purplish tint, especially as teliospores germinate. Teliospores double, oval, each of the two cells globular and equal, constricted at septum; 10–15 μ by 25–34 μ (fig. 6). Wall chocolate-brown, 1.0 to 1.5 μ thick, uniform, continuous, and smooth with faint lateral indentation; pores at septum and toward apex. Pedicel short, fragile, and deciduous, very rarely observed in uredia early in summer. Teliospores germinate when mature and moist; promycelium septate, basidiospores sessile, round, 10–15 μ in diameter, hyaline, fragile, with no surface sculpturing.

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TORREYA

LYSICHITON VERSUS LYSICHITUM

The name of this genus of Aroids has, since the original description by Schott in Oester. Bot. Wochenb. **7**: 62, 1857, been given one or the other of these two spellings with about equal frequency. Since Hulten and St. John described the American species, *L. americanum*, in Svensk Bot. Tidskr. **25**: 453–464. 1931 using the "um" ending, this spelling has been used more frequently. These authors justified their stand by stating that *Lysichiton* was a later spelling. Investigation of Schott's original description, however, reveals that this is not the case. The description itself is preceded by a justificatory paragraph. In the final sentence of this paragraph Schott stated that he proposed to call the new genus *Lysichiton*. Following this, the description was preceded by the spelling *Lysichitum*.

I made a survey of Schott's succeeding writings to see if perhaps he, himself, could have settled the question. "Genera Aroidearum" was published in 1858, the year following the description. In it, Schott introduced the discussion of the genus by the spelling *Lysichitum*. In the discussion, on the other hand, he listed the only known species as *Lysichiton camtschaticum*. The name is spelled *Lysichiton* in the two other of Schott's works in which the genus is mentioned. These works are, "Prodromus Systematis Aroidearum", 1860, and "Araceae: Nova Genera et Species" in Miquel's "Ann. Mus. Bot. Lugd. Bat." **1**: 285. 1864. Therefore, it appears that he finally settled on this spelling.

Though Article 83 of the International Rules of Botanical Nomenclature, 1952 edition, mentions only Linnaeus, the rule would seem to apply in this case. It states that when the spelling of a generic name differs in Linnaeus' Sp. Pl. ed. 1 and Gen. Pl. ed. 5 and Linnaeus subsequently and consistently adopted one of them, that spelling is accepted. Further it states that if one of the spellings is philologically more correct, that spelling should have preference. Since *Lysichiton* is a Greek word and "on" the Greek ending, this would be the more correct spelling.—DONALD G. HUTTLESTON, Brooklyn Botanic Garden.

FIELD TRIP REPORTS

July 10–11, Pine Barren week-end, N. J. The water table was extremely low and the group was able to walk across dry sphagnum moss and white water lily pads with ease in the vicinity of Quaker Bridge. A large station (about one-half acre) of the rare and local *Rhyncospora oligantha* was found and, in addition, a few specimens of *Eriophorum tenellum*, past prime. Attendance 37. Leaders, David Fables, Frank Hirst and Robert Leisy.

July 27, High Point State Park, N. J. The prolonged drought had markedly affected the fern and orchid flora in this region. Mr. and Mrs. Hallett located a most interesting station of several species of *Botrychium* near their summer home adjacent to High Point Park. These included *B. lanceolatum*, *B. matricariaefolium*, and *B. simplex*. Most of the specimens were in a wilted state and much under normal size. *Malaxis unifolia*, difficult to detect among numerous cinnamon ferns, was found at two stations. The most prevalent orchid of the day was *Habenaria clavellata*. Attendance 12. Leader, David Fables.

August 7, Huntsburg, N. J. Hunt's pond is being developed and the future of the flora is in doubt. Among the species found growing there at this date were *Najas flexilis*, *Najas gracillima*, *Heteranthera dubia*, *Eriocaulon septangulare* and *Isoetes echinospora*. *Sagittaria coneata* was found in abundance at a pond near Huntsburg, the only known station for it in New Jersey. In a small cat-tail marsh near Greendel

Potentilla palustris was located, but there were no blossoms. Attendance 26. Leader, J. L. Edwards.

August 18, Stokes Forest, N. J. The station for *Habenaria psycodes* had been reduced to one specimen. There was no evidence of deer browsing as there is so often in the Forest. A station for *Lycopodium inundatum*, under observation for several years in Swenson Fields appears to be shrinking in size. Many of the plants resemble *L. alopecuroides* and *L. adpressum* of the Coastal Plain. Whether they are these species or not is unknown, but J. L. Edwards believes they may all prove to be *L. inundatum*. He feels study of the genus is needed and perhaps revision is in order. Attendance 7. Leader, David Fables.

Sept. 12, 1954. Reading Region, Berks Co., Pa. Various habitats Oley Valley to Maiden Creek and shore of Lake Ontelaunee were visited. Plants seen that are rather rare or local in the Torrey range include: *Pinus pungens, Eragrostis Frankii, E. hypnoides, Campanula americana, Polymnia Uvedalia, Silphium perfoliatum, Coronilla varia, Kuhnia eupatorioides,* and *Aster sagittifolius.* Especially fine colonies of *Cheilanthes lanosa, Woodsia ilvensis* and *Pellaea glabella* were seen, as were a few plants of *Selaginella rupestris* and *Camptosorus rhizophyllus.* Two grasses of relatively recent introduction also occur in this region. *Eulalia viminea* var. *variabiles,* which is rapidly spreading through S.E. Pa. and southward, and *Manisuris altissima,* which has appeared at several stations in Berks Co. but known elsewhere (in the U.S.) only from southern Texas. Attendance 3. Leader, Hans Wilkins. Reported by L. E. Hand.

Oct. 9–10. Pocono Mt., Pa. On Saturday the Tannersville bog was explored and the usual components of a spruce-larch bog were seen, such as *Andromeda glaucophylla, Kalmia polifolia, Vaccinium Oxycoccus, Carex trisperma, Sarracenia purpurea,* etc. Mention should also be made of the occurrence of *Menyanthes trifoliata* and *Arceuthobium pusillum.* Rest of the day was devoted to searching for fossils at various locations in Monroe Co. and much time was spent examining the coral reef near Analomink, with its abundance of early fossils.

On Sunday we drove to the former site of Tannersville station, where a few early plant fossils were found. From here we drove for 2 miles over the cinder bed of the abandoned Wilkes-Barre and Eastern R. R. and then up the regular road to the summit of Big Pocono Mt. The vegetation at the summit is of the barren type with much bear oak, vacciniums, etc. all of low stature. Near the foot of Big Pocono, the large *Tilia americana* was examined. It is now in poor condition, having recently lost a large limb 92½ inches in circumference from about 15 ft. up, and the interior of the tree is well rotted out. The tree is estimated to be over 350 years old, and in 1947 was considered the largest in the U.S.A. Attendance 13. Leader, L. E. Hand.

October 30, Long Branch to Toms River, N. J. Gannets, both immature and adult, were observed offshore at Manasquan Inlet. Ducks were abundant on most of the ponds, the scarcer species included European widgeon, redhead and canvasback. Outstanding species though were the terns, the caspian, which gave us an excellent opportunity to study it from a few feet, at Old Sam's Pond, Point Pleasant, and two royal terns seen at Manasquan Inlet. Both are rare in the State. Attendance 32. Leader, David Fables.

No further reports of 1954 field trips will be published. Please send in reports of 1955 excursions promptly. They are more interesting and profitable for study if the chronological sequence is maintained.—J. A. S.

Book Reviews

Grasses. By C. E. Hubbard. xii + 428 pp., illustrated. A Pelican Book, Penguin, London, 1954.

British botanists have long been known for their clarity in expression and exactitude in description. At the same time they have done more than their English-speaking colleagues abroad to popularize science in a commendable way without loss

of scientific accuracy. In recent years there have been published in Britain several books about natural history which equal the best popular and scientific publications in the world; and three years ago the most modern flora of the day was printed in England—Flora of the British Isles, Cambridge 1952.

In spite of the fact that the new British Flora is highly modern and very informative, the botanists of this island continue their search for more knowledge and do not cease to produce still better manuals. The last handbook in the recent series of first-class botanical publications from England is a handbook on the British grasses compiled and written by C. E. Hubbard of the Herbarium of the renowned Kew Gardens, with excellent illustrations by Joan Sampson. It is a Pelican Book, 428 pages with detailed pictures of 152 species of grasses and several explanatory figures in the text, and its price is only 3 sh 6d, or the equivalent of about 50 cents!

The book begins with introductory information on the structure of the grasses and explanations on how to use the keys and find the correct species in the manual. It ends with chapters describing the uses of grasses and their relatives, other pertinent information and a good glossary. But most of the book is devoted to descriptions of the individual species—one page of illustrations and one page of description for each—as well as keys for their determination on the basis of floral and vegetative characters or of their fruits alone.

The author is modern though conservative in his nomenclature. For example: in the one genus *Bromus* are included all groups of that composite genus, and the genus *Agropyron* here includes the taxa perhaps more accurately classified as the genera *Roegneria* and *Elytrigia*. He does not hesitate to accept the separation of *Elytrigia junceiformis* from *E. juncea*, *Aira multiculmis* from *A. caryophyllea*, and *Phleum commutatum* from *P. alpinum* as modern cytotaxonomists have done, although he sometimes classes some equally good species as only races, e.g., *Agrostis canina* ssp. *montana* (=*A. hyperborea* Laest.). As a whole, however, the species and generic concept of Mr. Hubbard is that of the experimentalists, although he himself is a herbarium botanist first and foremost, thus showing the strong trend towards biosystematics so prominent among British botanists of to-day.

Although this excellent book by Mr. Hubbard is written mainly for inhabitants of and visitors to Britain, it is highly recommendable to all those on this side of the Atlantic interested in different aspects of the grasses. It cannot replace the good but somewhat old-fashioned Manual of the Grasses of the United States by Hitchcock and Chase, since not all the American grasses occur in the British Isles, but it can serve as a substantial complement to the American manual. All those interested in grasses and working with them will benefit much from its modern treatment, and no botanically interested person should visit England without this most useful and surprisingly inexpensive handbook.—ÁSKELL LÖVE, University of Manitoba.

Sex in Microorganisms. A symposium presented on December 30, 1951 at the Philadelphia meeting of the American Association for the Advancement of Science. Editorial Committee—D. H. Wenrich, I. F. Lewis, and J. R. Raper. American Association for the Advancement of Science 1515 Massachusetts Ave. N.W., Washington 5, D. C. 1954. $5.75 ($5.00 to members).

Ten papers describing available evidence for the phenomenon of sex in the principal groups of microorganisms are included in the symposium. The first paper by Visconti discusses evidence for recombination of "genes" in bacteriophage. Present data suggest that these viruses do not possess any activity analogous to sex, but, that through a study of their genetics, bacteriophages may offer an important tool in the explanation of the main features in virus reproduction. Sex phenomena in bacteria are discussed by Lederberg and Tatum and by Hutchinson and Stempen. The former authors present genetical evidence and studies of *Escherichia coli* which show that in

mixed cultures under suitable conditions a small but significant number of cells of certain strains undergo a process of recombination of genes governing a wide variety of characters. This process apparently involves some sexual relationship that may in the future correlate the genetic and morphological aspects of conjugation and meiosis in bacteria. The latter paper approaches the problem from a morphological viewpoint. Studies of fixed and stained cells and of photographs of these have allowed the observation of fusion in certain bacterial cells. It is not known whether this is a sexual process involving fusion and segregation of nuclear material.

One paper of the symposium is devoted to the study of sexual mechanisms in the fungi. Rapier presents a comprehensive review of the literature of their life-cycles, sexuality and sexual mechanisms. Present data are insufficient to permit the postulation of a completely feasible sexual situation now existing in the fungi. Sexual phenomena in the lower algae are reviewed by Patrick and by Lewin. The existence of other forms of reproduction than mitosis are admitted but insufficient evidence exists, at present, for the determination of true sexual differentiation in algae.

A large portion of the symposium is devoted to sex in protozoa. A comprehensive review is presented by Wenrich. Sexual phenomena are described for the *Phytomastigina, Zoomastigina, Sarcodina, Sporozoa,* and *Ciliaphora.* Specific studies in cellular heredity in *Paramecium* are discussed by Nanney. Mating type perpetuation through both vegetative and sexual reproduction is shown to be due to a series of nucleoplasmic interactions and is thus an active partner in cellular heredity. The physiology of fertilization in ciliates is described by Metz. Although many interesting experiments in the field are reported, the distribution and evolution of sex in protozoa is still in an uncertain state.

The concluding section of the symposium presents comments on the origin and evolution of sex, especially in protozoa. This volume brings together most of the pertinent material presently available on sexual phenomena in microorganisms and is therefore an excellent reference book. However, conclusive proof for the existence of sexual phenomena in microorganisms does not as yet exist.—ISABEL R. DIMMICK, Assistant Professor of Bacteriology, Douglas College, Rutgers University, The State University of New Jersey, New Brunswick, New Jersey.

Indian Corn in Old America. By Paul Weatherwax. xii + 253 pages; figs. 1–75. The Macmillan Company, N. Y. 1954. $7.50.

Indian Corn in Old America tells the story of corn from the days of the Incas and Mayas down to the modern era. The interdependence of the American Indian and corn is brought out in the description of the economy and culture of these tribes and the prominent place occupied by corn in their every day life and artistic expressions. This is an excellent book, well illustrated with sketches and photographs. It is a revision of an earlier edition by a competent author.

The first four chapters treat rather fully the historical records of where the corn plant was first observed, how it was described by the various explorers, beginning with Columbus and the various names originally given the plant. The origin of the word "maize" is discussed but whether it is called corn, Indian corn, maize or *Zea mays,* it is all the same plant. Numerous sketches and drawings from these old accounts are presented.

A brief account of how corn first went to Europe and how it was received is given in the next chapters. Apparently corn was brought back when Columbus returned from either his first or second voyage. According to these early reports corn was first grown by the Europeans as an agricultural oddity but within a few years it began to assume economic importance in southern Europe. The plant was of considerable interest to the European botanists.

Where and how corn was grown in Old America is discussed in Chapters 7 and 8. The early explorers found corn in an area that is now the United States, southward through Mexico, Central America and in much of South America. Early records are

listed giving some details as to who found corn growing in various areas mentioned. Apparently there were three main centers of corn cultivation, one on the Mexican plateau, one in Yucatan and Guatemala and one in Peru which corresponded to the three pre-Columbian civilizations, Aztec, Mayan and Incaic. The desert had much to recommend it over the grassy prairies for agricultural purposes of primitive man. The first important factors noted in describing how corn was grown are the handicaps of not knowing about iron and tools and not having domesticated draft animals. Very interesting discussions are given on the various methods of soil preparation, determining the time to plant, methods of planting, cultivation, harvesting and storage. Throughout these discussions it is pointed out how much progress had been accomplished by certain tribes in their corn production methods.

The early white explorers were impressed by the fact that corn produced food in such an efficient manner, and made reference to this fact in many of their early reports and accounts. Much of the information about the uses of corn as a food was obtained by studying the many stone devices used for grinding. These are described and shown by excellent photographs. Other uses of corn included alcoholic drinks, forage for animals, husks for various uses, utilization of silks, cobs and stalks for various purposes and finally the use of corn as currency.

Many of the problems of the American Indian in producing corn are still present today. One was the conservation of the corn lands. Early efforts of conservation included types of rotations, the use of manures and ashes, and of particular importance, the use of terracing and irrigation. Some of these systems of terraces and irrigation are among the most amazing agricultural engineering feats of all times especially so since they were constructed by hand.

The unanswered question as to the possible origin and relatives of such an important plant as corn is treated very well. The possibility that corn crossed the Pacific and was well established in Asia long before 1492 is discussed as well as other references to Asiatic corn varieties. At present, there is no unmistakable direct evidence as to what sort of plant wild corn was, where it grew or under what conditions domestication began. This lack of direct information as to the origin of corn places more emphasis on the botanical evidences which are discussed. The close relationship among the American genera, *Zea*, *Tripsacum* and *Euchlaena* is recognized but the difficulties of producing hybrids among them is pointed out. The short comings of pod corn as an ancestor of cultivated corn are also listed.

The various theories of hybrid origin advanced by several investigators are discussed and their good and bad points noted. The simple conservative view that the three related genera, *Zea*, *Tripsacum* and *Euchlaena*, descended from some common ancestor by divergent evolution is discussed. This assumption brings in the question of isolating mechanisms that would have been necessary for these three plants to arise from a common ancestor. The role of domestication is suggested as a reasonable mechanism that became operative somewhere in the evolution of corn. Apparently the American Indian took advantage of the high mutation rate in corn during domestication. The emphasis on the individual plant, contrasted to smaller cereals, was no doubt one important factor responsible for many changes in the plant. Variations in vegetative character, ear form and structure, grain morphology, endosperm characters, and kernel colors of the early corn varieties are discussed. Many excellent illustrations accompany these discussions.

The concluding chapters stress again the very close association which existed in the past and exists to a large extent today between the Indian and the corn plant. Evidence is presented showing that the Indian had many thoughts and practices related to corn which digressed far from purely utilitarian consideration. The contribution of the American Indian to our world agriculture is summarized as follows: "One net result of his work through the centuries was to take from the undomesticated state a plastic grass plant, and by processes as mysterious as they were effective, to convert it into the most versatile and adaptive of all cereals, a plant so efficient in turning raw resources into food and other useful materials that it dominated ancient American agriculture for thousands of years and has since gone on to extend its influence all over the world" (page 238).—J. W. COLLIER, Rutgers, The State University of New Jersey.

Important Trees of the Ryukyu Islands. By Egbert H. Walker. Special Bulletin (United States Civil Administration of the Ryukyu Islands) no. 3, vi + 350 pp. 209 figs. 1954.

This is a treatment in Japanese and English of 207 species of native and introduced trees selected by Okinawan botanists as important in the economy of the Ryukyu Islands. It was prepared at the request of the foresters of the U. S. Civil Administration to aid their program of improvement of conditions of life in these islands toward greater self-sufficiency of the people. It is a joint production of the U. S. Army and the Pacific Science Board of the National Research Council through their program of Scientific Investigation in the Ryukyu Islands, with contributions by the Smithsonian Institution. The work stresses identification and economic uses, with emphasis on the wood characteristics. Each species is illustrated with a line drawing. The bilingual presentation in parallel columns is a unique feature in the literature in this country, and is one which will make this work of real use to the Ryukyu foresters, students, and people generally, as well as to the many Americans stationed there. The work is excellently published by the U. S. Army in Okinawa and is bound with a stiff cover. Copies may be obtained on request addressed to the Office of Civil Affairs and Military Government (OCAMG), The Pentagon, Washington 25, D. C. (Attention Col. J. S. Harbison), or, for those in the Far East, from Central Information & Education (CI&E), U.S.C.A.R. APO 719, San Francisco, California, or (USCAR, Naha, Okinawa).—E. H. WALKER, Smithsonian Institution.

The Polyporaceae of the United States, Alaska and Canada. By L. O. Overholts. Prepared for publication by Josiah L. Lowe. 446 pp., 132 pls. University of Michigan Press. Ann Arbor, 1953. Price $7.50.

Considering their function in nature, the polypore fungi are no doubt one of the most important groups of plants. Everywhere there is living or dead wood, they are the most active agents of decomposition. Hence, the need of an elaborate taxonomic account on the numerous species of this family occurring in a large area like North America was eagerly felt, especially by forest pathologists. Although quite a number of systematic treatments have been published on this group in this part of the world since Peck, a modern book, including most of the more recent information and revisions of the status of many species was an urgent necessity. To this life-time task Dr. Overholts assigned himself more than five decades ago. For this purpose, he gathered large amounts of material with photographs and notes in an extensive territory covering most of the United States and parts of Canada and Alaska. The writing of this systematic arrangement was initiated more than 20 years ago, but until his death in 1946 he ceaselessly added new details and revised his manuscript.

In spite of his haste to complete this valuable contribution to science during his last years, he could not see it published. Without the efforts of Dr. Lowe of the University of New York State (Syracuse), who was closely associated with Dr. Overholts in the study of the Polyporaceae, the results of half a century of work and experience would have been lost or at least not easily available. Therefore, all students of the polypores should be grateful to Dr. Lowe for the final arrangement of this monumental publication and to the editor who is responsible for the fine presentation of this manual.

This descriptive treatment of some 235 species of pileate polypores is probably a land-mark in the mycological literature of North America. For mycologists and forest pathologists it represents one of the most up-to-date working tools. The comprehensive keys and the concise but complete diagnoses are all based on the author's own experience. One of the greater merits of this book is no doubt the extensive illustrations with some 675 photographs and a number of drawings distributed in 132 plates. With such a manual it is now possible to identify most of the species of pileate polypores occurring in North America.

With regard to the taxonomic arrangement of species adopted by the author, he was

certainly conservative as he himself admitted. He did not attempt to segregate the old genera *Polyporus* and *Fomes* as is often done by European and a few American authors. To be sure, a few genera such as *Ganoderma, Unguilina* and *Melanopus* are now well characterized. But, on the other hand, others such as *Coriolus, Polystictus, Leptoporus,* etc. are quite differently interpreted by various authors. Dr. Overholts has therefore enough justification for his reluctance to accept a new grouping. As it is, this book with its splendid illustrations is the best practical approach for the identification of species of pileate polypores.—RENÉ POMERLEAU, Laval University, Quebec City.

NOTES

Dr. Liberty Hyde Bailey, Dean Emeritus of the State College of Agriculture at Cornell, died at his home in Ithaca on Christmas eve, 1954. He had served Cornell well over half a century as professor, dean and, more recently, as Director of the Bailey Hortorium. Dr. Bailey was 96 years old.

Mr. Wallace M. Husk died in Rahway Hospital the evening of November 23, 1954. Mr. Husk will long be remembered for his hospitality in arranging accommodations for the Branchville Nature Conference over a period of several years.

"Bibliography of Free and Inexpensive Materials for Teaching Conservation and Resource-use" (second edition) by Muriel Beuschlein has been published by the Conservation Project of the National Association of Biology Teachers. Copies are 10¢ with 20% discount on 100 or more from Dr. Richard L. Weaver, P. O. Box 2073, Ann Arbor, Michigan. This bibliography will be Chapter XII of the "Handbook on Teaching Conservation and Resource Use" to be published early in 1955. The Handbook sells for $4.00, with 20% discount to teachers and schools. It may be ordered from Dr. Weaver.

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LAZELLA SCHWARTEN

(WITH THE COLLABORATION OF THE EDITORS OF THE TAXONOMIC INDEX)

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